MYCOLOGIA

Official Organ of the Mycological Society of America

Vol. LIII　　July-August, 1961　　No. 4

CONTENTS

[Mycologia for May–June, 1961 (53: 215–316) was issued April 18, 1962]

PUBLISHED BIMONTHLY FOR

THE NEW YORK BOTANICAL GARDEN

AT PRINCE AND LEMON STS., LANCASTER, PA.

Second-class postage paid at Lancaster, Pa.

MYCOLOGIA

Published by

THE NEW YORK BOTANICAL GARDEN

IN COLLABORATION WITH THE

MYCOLOGICAL SOCIETY OF AMERICA

ANNOUNCEMENTS

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(Continued)

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MYCOLOGIA

OFFICIAL ORGAN OF THE MYCOLOGICAL SOCIETY OF AMERICA

VOL. LIII JULY-AUGUST, 1961 No. 4

STUDIES OF SOME TREMELLACEAE. IV. EXIDIOPSIS[1,2]

KENNETH WELLS

(WITH 13 FIGURES)

The genus *Exidiopsis* was originally defined by Johan-Olsen (apud Brefeld, **1888**) as a subgenus of *Exidia* to include a single species, "*Exidiopsis effusa* Bref."[3] This species was characterized by Brefeld as differing from the remaining species of *Exidia* by the effused form, but similar in that the basidia, the basidiospores, and the structures formed during the germination of the basidiospores were similar to such structures found in the genus *Exidia*. One of the more important taxonomic characters of *Exidia*, in Brefeld's opinion, was the formation of "kreisformig umgebogenen Conidien" during the germination of the basidiospores. Such conidia, according to Brefeld, are formed by the germinating basidiospores of "*Exidiopsis effusa*." *Exidiopsis* was elevated to the rank of genus by Möller (**1895**). Möller retained Johan-Olsen's concept of the group and described five additional species. One, *Exidiopsis cerina* Möll., is almost certainly to be included in the genus *Bourdotia*, while two of the species were transferred to the genus *Hetero-*

[1] The first report of this series appeared in Lloydia **20**: 43–65; the second, which treated the genus *Ductifera*, in Mycologia **50**: 407–416; and the third, dealing with the genus *Bourdotia*, in Mycologia **51**: 541–563.

[2] Portions of this study were supported by a grant from the National Science Foundation.

[3] *Exidiopsis* was published as a subgenus, hence the combination *Exidiopsis effusa* Bref. was not validly published (Art. 42, Intern. Code Bot. Nomenclature, 1956).

[MYCOLOGIA for May–June, 1961 (**53**: 215–316) was issued April 18, 1962]

chaete by Bodman (**1952**). The remaining species are treated in this report. In addition, Möller described the genus *Stypella* to include those resupinate, tremellaceous species which consist of scattered or densely gregarious, fertile papillae connected by a delicate subiculum; and *Protohydnum* for those species forming tremellaceous basidia on resupinate, *Hydnum*-like basidiocarps. Möller also recognized the genus *Heterochaete,* which had been established by Patouillard (apud Patouillard and Lagerheim, **1892**) to include the resupinate, tremellaceous fungi with fascicles of sterile hyphae piercing the hymenium.

Other genera which are closely related or thought to be closely related to *Exidiopsis* and are pertinent to the present report are: *Sebacina,* established by L. R. and C. Tulasne (**1871**) with *Corticium incrustans* Pers. considered (McGuire, **1941**; Martin, **1952**; Ervin, **1957**) as the type species; *Heterochaetella,* established first as a subgenus by Bourdot (**1921**) and later elevated to the rank of genus by Bourdot and Galzin (**1928**) with *Heterochaete dubia* Bourd. & Galz. selected (Ervin, **1957**; Donk, **1958**) as the type; *Bourdotia,* elevated to generic rank (Ervin, **1957**; Wells, **1960**; see, however, Donk, **1958**) by Bresadola and Torrend (apud Torrend, **1913**) with *Sebacina galzinii* Bres. as the type; *Eichleriella,* established by Bresadola (**1903**) with *Eichleriella incarnata* Bres. selected (Burt, **1915**; Martin, **1952**) as the type; *Tremellodendron,* established by Atkinson (**1902**) with *Merisma candidum* Schw. selected (Burt, **1915**; Martin, **1952**) as the type; *Hirneolina,* established as a section of *Sebacina* by Patouillard (**1900**) and later elevated to generic rank by Bresadola (apud Saccardo, **1905**) with *Sebacina hirneoloides* Pat. as the type; and *Protodontia,* established as a genus by Höhnel (**1907**) for *Protodontia uda* Höhn.

The taxonomic treatments of the resupinate species of the Tremellaceae have been varied. Patouillard (**1900**) recognized *Sebacina* and *Heterochaete* as distinct genera and divided *Sebacina* into four sections; i.e., *Stypella, Exidiopsis, Hirneolina,* and a section containing the incrusting species. Burt (**1915**) treated *Eichleriella* and *Sebacina* as distinct genera and listed *Exidiopsis* and *Stypella* as synonyms of *Sebacina.* Rea (**1922**) recognized *Sebacina* as being composed of three subgenera; i.e., *Bourdotia, Heterochaetella,* and *Eusebacina.* He considered *Eichleriella* as a distinct genus. Bourdot and Galzin (**1928**) treated *Sebacina, Eichleriella, Bourdotia,* and *Heterochaetella* as separate genera. These authors divided the genus *Sebacina* into two sections; i.e., *Exidiopsis* and *Viscosae.* Killermann (**1928**) treated *Heterochaetella* as a subgenus of *Heterochaete.* The genus *Sebacina* was separated by Killermann into two subgenera; i.e., *Bourdotia* and *Tremellodendron.* Killer-

mann recognized *Exidiopsis* as a distinct genus. Donk (**1931**), in his treatment of the Heterobasidiomycetidae of the Netherlands, recorded *Bourdotia* and *Sebacina* as distinct genera. He regarded *Exidiopsis* as synonymous with *Sebacina.* Clements and Shear (**1931**) recognized *Heterochaete,* listing *Heterochaetella* as a synonym; *Hirneolina,* listing *Eichleriella* as a synonym; *Sebacina* to include *Bourdotia* and *Tremellodendron; Stypella;* and *Exidiopsis.* McGuire (**1941**), in his study of the North American species of *Sebacina,* divided the genus into three sections; i.e., *Eusebacina, Heterochaetella,* and *Bourdotia.* He postulated that *Sebacina* was distinct from *Tremellodendron, Stypella,* and *Eichleriella.* Martin (**1952**) followed McGuire in his treatment of the genus *Sebacina,* but remarked that the genus, as defined by McGuire, was a heterogenous assemblage. Moreau (**1953**) recognized *Hirneolina, Sebacina, Exidiopsis, Stypella,* and *Heterochaete* as distinct genera. He did not mention the other genera considered here. Christiansen (**1959**), in his study of the Danish species, followed McGuire (**1941**).

In a recent study of *Sebacina* and related genera, Ervin (**1957**) restricted the genus *Sebacina* to the type species, *Sebacina incrustans* (Pers. ex Fries) Tul., and two closely related species, *Sebacina helvelloides* (Schw.) Burt and *Sebacina epigaea* (Berk. & Br.) Rea. Ervin retained the concept that *Tremellodendron* is distinct from these species and redefined the genus *Exidiopsis* to include the resupinate, nongloeocystidiate species with clamp-connections throughout the fructifications. Ervin recognized *Bourdotia* and *Heterochaetella* as worthy of generic rank.

In his treatment of the Heterobasidiomycetidae of Tahiti, Olive (**1958**) recognized *Stypella, Sebacina,* and *Heterochaete* as distinct genera. He followed McGuire in segregating *Sebacina* into three sections; i.e., *Eusebacina, Bourdotia,* and *Heterochaetella.*

Luck-Allen (**1959**), in a report of her studies of several resupinate, tremellaceous genera, indicated that she intended to recognize *Heterochaetella; Stypella; Eichleriella; Sebacina,* in a restricted sense; and *Exidiopsis.* Since *Bourdotia galzinii* (Bres.) Bres. & Torr. was to be included in *Exidiopsis,* another generic name is to be selected by Luck-Allen for the remaining species of *Bourdotia.* Luck-Allen (**1960**) more recently presented a detailed account of *Heterochaetella.*

My own morphological studies of a number of specimens of resupinate and near-resupinate species of the Tremellaceae have indicated a number of natural groups, which, in several cases, are not delimited by the presently accepted genera. Thus, in my opinion, a number of genera need to be redefined in order to more nearly approach a natural system of

classification. It appears that basidial structure and internal structure of the basidiocarp are characters of prime taxonomic importance in these groups, and basidiocarp form should be considered of secondary importance.

The genus *Bourdotia* and its possible relationships with other tremellaceous genera have been previously considered (Wells, **1960**) and need not be discussed at this time.

The genus Sebacina, as defined by Ervin (**1957**), is, in my opinion, a natural group.[4] The general lack of clamp-connections throughout the basidiocarps, especially at the base of the basidia, and the cartilaginous to coriaceous texture, apparently resulting from the tendency of the subhymenial hyphae to become thick-walled, are indicative of a natural series. Olive (**1958**) has objected to Ervin's definition of the genus *Sebacina*. He pointed out that the basidiocarps of *Sebacina epigaea* may be gelatinous or waxy-gelatinous; however, I would add that older specimens become less pliable and closely approach the texture of *S. helvelloides*. It is my impression that sub-basidial clamp-connections are a consistent feature of *Exidiopsis*, as I would define the genus, and that such structures are lacking in *Sebacina* s. str. Even though, as Olive states, the presence or absence of clamp-connections is often a variable feature within a species, it is, I think, of sufficient consistency in *Sebacina*, sensu Ervin, and *Exidiopsis*, sensu Wells, to be used as a generic character. Therefore, I feel that *Sebacina epigaea, S. helvelloides, S. incrustans*, and *Tremella concrescens* form a natural group which is sufficiently distinct to warrant generic status. Further, because of similarities in basidial and hyphal structure, it would appear that this group is more closely allied with *Tremellodendron* than with *Exidiopsis*.

Another natural group is distinguished primarily by sphaeropedunculate basidia which become separated into globose, nucleated, apical portions and basal, enucleated, cylindrical stalks. It has been stated (e.g., McGuire, **1941**, and Wells, **1957**, for *Sebacina podlachica* Bres.) that the apical, globose portion of the sphaeropedunculate basidium becomes separated from the basal stalk by the formation of a secondary septum which is differentiated without a clamp-connection; however, I have not been able to demonstrate this feature with the basidia of *Exidia nucleata* (Schw.) Burt using aceto-carmine or other nuclear stains. The formation of septa in the sphaeropedunculate basidia of *E. nucleata* and related species is not clear and deserves additional study. I have noted such basidia in *E. nucleata, Sebacina podlachica, Stypella minor* Möll., *Sty-*

[4] Dr. Robert J. Bandoni has suggested (personal communication) that *Tremella concrescens* (Fries) Burt belongs in this group. I concur in his opinion.

pella papillata Möll., *Protodontia uda* Höhn., and *Protodontia piceicola* (Kühner) Martin. Although I earlier reported (Wells, **1957**) that *Sebacina sublilacina* Martin does not have sphaeropedunculate basidia, careful examinations of the type specimen and numerous fresh specimens have shown that sphaeropedunculate basidia are a consistent character of this species. Luck-Allen's (**1960**) drawings of *Heterochaetella dubia* and my own limited observations indicate that such basidia are also present in this species. Other features of certain species also tend to indicate a natural relationship. Some specimens of *Exidia nucleata, Sebacina podlachica,* and *S. sublilacina* have large, white, mineral accumulations. The hyphae and basidia of *Heterochaetella dubia, Stypella minor, S. papillata,* and *Sebacina sublilacina* become agglutinate upon drying. This latter character is found in varying degrees in other species of the group. If one considers these species naturally related, then the thin-walled cystidia of *Sebacina sublilacina,* the thick-walled cystidia of *Heterochaetella dubia,* and the thin-walled, gloeocystidiate structures of *Stypella papillata* may be considered homologous hymenial elements. Further, many of the basidiocarps of the species are pustular in origin. The basidiocarps of *Exidia nucleata* become cerebriform and erumpent but are initially small, hyaline pustules. Certain specimens of *Sebacina sublilacina* reveal a pustular nature in cross section, and most specimens of *Stypella minor* and *S. papillata* are tuberculate. The downward-directed "teeth" of the species of *Protodontia* are more highly specialized but are, nevertheless, akin to the pustules of the other species. Whether or not one or more genera should be recognized within this group can be decided only after additional studies.

A third series is also distinguished by basidial characters. *Eichleriella spinulosa* (Berk. & Curt.) Burt, *Heterochaete delicata* (Kl. ex Berk.) Bres., *Heterochaete livido-fusca* Pat., and *Protohydnum cartilagineum* Möll. have large clavate basidia in which longitudinal septa apparently diverge in basal regions to delimit short, sterile stalks. All of these species have basidiocarps of essentially the same texture, and spines of varying sizes are formed in most of the basidiocarps. Although the basidiocarps of *Tremellodendropsis* (Corner) Crawford (Crawford, **1954**) appear similar to those of *Tremellodendron* macroscopically, the basidial structure and hyphal characters are indicative of a relationship with *Eichleriella spinulosa* and related species. *Bourdotia petiolata* (Rogers) Wells has basidia similar to those of this group; however, other characters indicate that this species should be retained in *Bourdotia.*

The genus *Eichleriella* Bres., as defined to include those tremellaceous species with tough to coriaceous basidiocarps which are broadly effused

with abrupt margins or which are cupulate, does not include a naturally related group of species. The type species, *E. incarnata* [= *Eichleriella alliciens* (Berk. & Cke.) Burt], and *Eichleriella macrospora* (Ell. & Everh.) Martin seem best included in *Exidiopsis*. *Sebacina hirneoloides* Pat., the type species of *Hirneolina*, is possibly a member of the genus *Heterochaete* Pat., as defined by Bodman (**1952**). Neither *Eichleriella gelatinosa* Murrill nor *Eichleriella leveilliana* (Berk. & Curt.) Burt appears to belong to any well known genus.

As defined in this study, the genus *Exidiopsis* is a somewhat divergent taxon, although not as heterogenous as the genus *Sebacina* as defined by McGuire (**1941**). There appear to be four groups, none sufficiently distinct to warrant generic segregation. One group is composed of *Exidiopsis calospora* Bourd. & Galz. and *Exidiopsis prolifera* (Rogers) Ervin. These species appear to be closely related, as indicated by the similarity in the morphology of the fertile hyphae, basidia, and basidiospores, and by the simplicity of the structure of the basidiocarps.

Exidiopsis molybdea (McGuire) Ervin, *Exidiopsis glaira* (Lloyd) Wells, and *Sebacina candida* Olive comprise a second group in which the fertile hyphae form basidia subtended by conspicuous, loop-like clamp-connections. The basidiospores of these species are often *Tremella*-like, which, in addition to the similarity in texture, indicates a relationship with the genus *Tremella*. In my opinion, however, these species should be retained in the genus *Exidiopsis* because of their affinities with such species as *Exidiopsis fugacissima* (Bourd. & Galz.) Sacc. & Trott. and *Exidiopsis grisea* (Pers.) Bourd. & Maire, which have similar basidial and fertile hyphal characters but differ in the structure of the basidiospores.

Exidiopsis fuliginea Rick forms a third group and is quite unlike most of the remaining species assigned to this genus, since the dikaryophyses in this species develop a yellow-granular content and disintegrate at maturity. Mature specimens of certain species of *Exidia*, such as *Exidia glandulosa* Fries, have dikaryophyses with a yellow-granular content.

Another group composed of the remaining species forms a related series terminating in the coriaceous species which may have reflexed margins upon drying. *Exidiopsis fugacissima* is the simplest member of this series, since the fructifications consist of a thin, basal layer from which the fertile hyphae arise; dikaryophyses are apparently lacking. *Sebacina laccata* Bourd. & Galz. and *Exidiopsis grisea* are examples of the more complex, waxy-gelatinous species of this series. *Sebacina calcea* (Pers.) Bres. and *Sebacina mucedinea* Pat. are arid-waxy in texture,

whereas *Eichleriella macrospora* and *Eichleriella alliciens* have a definite coriaceous texture. Throughout this series there is a gradual transition from the adnate, indeterminate margins of the thin, mucous-gelatinous species, such as *Exidiopsis fugacissima,* to the abrupt margins, which may become somewhat reflexed upon drying, of the coriaceous species, such as *Eichleriella alliciens.*

Certain of the thin, arid members of this group, such as *Heterochaete sublivida* Pat., which is here transferred to the genus *Exidiopsis,* and *Eichleriella macrospora,* show an affinity to certain arid species of the genus *Heterochaete,* from which they differ, however, in the lack of distinct, sterile, hyphal spines arising from the subhymenial region and piercing the hymenium. The distinction between *Exidiopsis,* as defined here, and *Heterochaete,* as defined by Bodman (**1952**), may not be natural; however, if *Heterochaete* is restricted to those species with sterile, hyphal spines arising beneath the hymenium, then *Exidiopsis* is distinguishable.

The basidiocarps of the species here assigned to the genus *Exidiopsis* are basically resupinate. In the simpler species, the basidiocarp may consist of only a few strands of hyphae parallel to the substrate, from which an ascending layer arises. The ascending layer, except in such species as *Eichleriella macrospora, E. alliciens,* and *E. leucophaea* Bres., is of varying width. The presence of collapsed basidia in the ascending layer and the variation of the width of the ascending layer, as seen in cross section, indicate that the thickness of the basidiocarp is of little taxonomic value. The thickness seems to depend, at least in the simpler species, on environmental factors and the age of the basidiocarp. The basidiocarps of the genus *Exidiopsis* appear to be indeterminate both as to thickness and width. The fertile hyphae are apparently capable of continuous formation of basidia by proliferations through or near the sub-basidial clamp-connections. In *Eichleriella macrospora, E. alliciens,* and *E. leucophaea,* and, to a varying degree, *Sebacina candida* and *Exidiopsis fuliginea,* there are well developed ascending layers without collapsed basidia.

Since this study was based largely on examinations of dried specimens, many of which have been in herbaria for a number of years, it is not possible to state with certainty that the hyphae of the subhymenial regions are always distinct. In freshly collected specimens and specimens collected in recent years, the subhymenial hyphae are distinct. Such hyphae have detectable clamp-connections throughout and in the more complex species become thick-walled. In such species as *Eichleriella macrospora* and *E. leucophaea,* the subhymenial hyphae are con-

sistently thick-walled in the specimens examined. In other species, such as *Exidiopsis molybdea,* the subhymenial hyphae of only the thicker specimens are thick-walled.

The dikaryophyses present in most species have a tendency to become indistinct in more mature specimens. Such species as *Exidiopsis calospora* and *E. prolifera* apparently do not form dikaryophyses. Other species, such as *Exidiopsis glaira* and *E. molybdea,* develop few dikaryophyses, and these soon become indistinct. Specimens of several species, such as *Exidiopsis grisea, E. fuliginea,* and *Sebacina candida,* may develop enlarged, subcylindrical, sterile elements in the hymenium; however, such structures are lacking or very sparse in many specimens assigned to the same species. Since these enlarged, sterile elements are not distinct morphological entities, they are here termed "cylindrical dikaryophyses." As noted by Olive (**1958**) in *Exidiopsis mucedinea* and by Wittlake (**1938**) in *Sebacina calcea,* there are structures present in the hymenium which are intermediate in size and shape between the cylindrical and the more numerous branching dikaryophyses.

The basidia of all species assigned to the genus *Exidiopsis* develop from or near sub-basidial clamp-connections in fundamentally the same manner as Rogers (**1936**) has described for *Exidiopsis prolifera.* Subsequent development is, of course varied. In most species the entire basidium becomes differentiated into two or four portions by longitudinal to oblique septa. In *Sebacina laccata,* and to a lesser degree in a few other species, an enucleate stalk is developed by the divergence of the longitudinal septa at the apex of the stalk (Wells, **1959**). In *S. laccata,* however, basidia are present which lack the stalk. The basidial terminology proposed by Martin (**1957**) is followed in this report.

The basidiospores are varied in morphology. The spores of *Exidiopsis calospora* and *E. prolifera* are long-fusiform or cylindrical-curved structures. Other species, such as *E. grisea,* have shorter, cylindrical-curved spores, while the spores of *Sebacina candida* and *Exidiopsis molybdea* are elliptical to subglobose. Although the basidiospores are quite varied within the genus, within a particular species the size and structure of the spores are excellent aids in identification. The basidiospores of all species are apparently capable of germinating by repetition. Under favorable environmental conditions, the basidiospores are presumably capable of direct formation of hyphae.

In my opinion, the taxonomic arrangement proposed in this and my previous papers is the closest approach to a natural system of classification that can be made on the basis of present information. These studies have been based exclusively on the morphology of the basidiocarps, and,

in several cases, the number of available specimens is probably not sufficient to characterize the species adequately. Several of the species can be cultured on artificial media; however, numerous attempts to induce sporulation, which would allow a considerable extension of our knowledge of the species and genus, have been unsuccessful.

I have attempted to consider all species which have been referred to *Sebacina, Exidiopsis,* or *Eichleriella,* especially those which have not been considered by Bodman (**1952**), Bourdot and Galzin (**1928**), Burt (**1915**), McGuire (**1941**), Rogers and Jackson (**1943**), or in my earlier reports on related genera.

The major portion of the specimens examined is deposited in the Herbarium of the Department of Botany at the State University of Iowa or in the Herbarium of the Department of Botany at the University of California, Davis. Many specimens from the personal herbarium of Professor D. P. Rogers of the Department of Botany, University of Illinois have been examined. Specimens which are not deposited in one of these herbaria are indicated by the use of the symbols recommended by Lanjouw and Stafleu (**1959**). Since numerous collections of Drs. R. J. Bandoni, G. W. Martin, D. P. Rogers, and my own were also examined, the appropriate initials are used to indicate these collectors.

ACKNOWLEDGMENTS

I am indebted to Dr. D. P. Rogers for his advice on nomenclatural problems, for the loan of numerous specimens, and for his valuable criticism of the manuscript; to Dr. R. J. Bandoni for many specimens and discussions pertaining to *Exidiopsis* and related genera; to Dr. A. L. Welden for several valuable specimens; to Dr. L. S. Olive for the loan of several type specimens; and to Dr. M. A. Donk for information concerning certain citations. Acknowledgments are due Dr. I. M. Lamb for the loan of specimens from the Farlow Herbarium; Drs. D. P. Rogers and C. T. Rogerson for the loan of specimens from The New York Botanical Garden; Mr. J. A. Stevenson and Dr. C. R. Benjamin for the loan of specimens from the National Fungus Collection; Professor R. Heim of the Muséum National d'Histoire Naturelle, Paris, for the loan of several type or authentic specimens; the Director, Naturhistoriska Riksmuseum, Stockholm, for the loan of several valuable specimens; the Director, Royal Botanic Garden, Kew for the loan of type specimens; Dr. J. C. Lindquist of the Instituto de Botánica C. Spegazzini, La Plata, for the loan of the type specimen of *Tremella sordida* Speg.; Dr. A. Skovsted of the Botanical Museum of the University of Copen-

hagen for the loan of the type specimen of *Sebacina microbasidia* Christiansen & Hauerslev; and Dr. J. N. Couch for the loan of specimens from the Herbarium of the University of North Carolina.

To Professor G. W. Martin, under whose direction I began the study of *Exidiopsis* and related genera, I extend special acknowledgments for his advice and helpful criticism, and for the loan of numerous specimens.

DESCRIPTION OF THE GENUS

EXIDIOPSIS (Joh.-Ols. ex Bref.) Möll., Protobas. 167. 1895.
Exidia subg. *Exidiopsis* Joh.-Ols. ex Bref., Unters. **7**: 94. 1888.
Eichleriella Bres., Ann. Mycol. **1**: 115. 1903.

Resupinate; margins adnate, effused, or abrupt; texture mucous- to waxy-gelatinous, arid-waxy, or coriaceous; fructifications often consisting of a horizontal hyphal layer of varying thickness giving rise to an ascending layer terminating in the hymenium; hyphae thin-walled with clamp-connections or becoming thick-walled; dikaryophyses present or absent; subcylindrical dikaryophyses, which arise in most cases from the fertile hyphae, sometimes present; fertile hyphae forming clusters of basidia by lateral proliferations through or near the sub-basidial clamp-connections; basidia subglobose, ovate, obovate, or clavate, becoming differentiated into 2–4 units by the formation of longitudinal or oblique septa; enucleate basidial stalks formed in some fructifications of certain species as a result of the divergence of the longitudinal septa; basidiospores germinating by repetition or by the formation of germination tubes.

Type: *Thelephora effusa* Bref. ex Sacc.

KEY TO SPECIES

a. Basidiospores more than four times as long as broad; dikaryophyses absent .... b.
a. Basidiospores less than four times as long as broad; dikaryophyses present or absent .... c.
 b. Basidiospores fusiform to sigmoid with attenuate apices, sometimes appearing branched, 17–35 × 2.5–5.5 μ .... 1. *E. calospora*
 b. Basidiospores cylindrical-curved to subhelicoid with blunt to attenuate apices, 18–27 × 2.5–4 μ .... 2. *E. prolifera*
c. Basidiocarps soft- to waxy-gelatinous or cartilaginous-gelatinous, usually effused, margins remaining attached upon drying, becoming evanescent or forming vernicose layer .... d.
c. Basidiocarps arid-waxy to coriaceous, usually with abrupt margins which may become reflexed upon drying, changing only slightly in thickness when moistened .... k.

d. Basidiospores subglobose, broadly obovate to ovate, or elliptical and ventrally depressed; basidia with conspicuous sub-basidial clamp-connections..e.

d. Basidiospores cylindrical-curved to allantoid; sub-basidial clamp-connections conspicuous to obscure..g.

e. Basidiospores subglobose to broadly obovate, rarely elliptical, 6–8 × 4–6 μ; basidia ovate to subglobose, 9–13 × 7–10.5 μ; known only from temperate regions..3. *E. glaira*

e. Basidiospores larger than 8 × 5 μ; basidia usually larger than 12 × 10 μ.......f.

f. Basidiospores subglobose, elliptical to cylindrical-curved, 10.5–19 × 5.5–8.5 μ; basidia 11.5–19.5 × 10–16.5 μ; basal regions of epibasidia 2–3.5 μ in diameter; known only from temperate regions.............4. *E. molybdea*

f. Basidiospores short-cylindrical, broadly elliptical to subglobose, 8–12.5 × 5–8 μ; basidia subglobose to pyriform, upon collapsing often becoming yellow-granular, 12–25.5 × 10.5–15.5 μ; basal regions of epibasidia 3–4.5 μ in diameter; known only from tropical and subtropical regions......... .... 5. *E. candida*

g. Basidiocarps mucous-gelatinous; basidiospores cylindrical-curved to obovate, 4.5–7 × 2.5–4 μ; basidia subglobose to obovate, 5–7 × 4.5–7 μ............. ....7. *E. fugacissima*

g. Basidiospores larger than 8 × 4 μ; basidia larger than 10 × 8 μ................h.

h. Dikaryophyses sparse, simple to little branched; basidiocarps mucous- to waxy-gelatinous; basidiospores cylindrical-curved to more frequently elliptical to subglobose..f.

h. Dikaryophyses abundant, especially in young specimens, branching or becoming brownish-granular; basidiocarps waxy- to cartilaginous-gelatinous; basidiospores mainly cylindrical-curved to allantoid.............i.

i. Dikaryophyses simple to little branched, becoming filled with brown granules and disintegrating; basidiospores cylindrical-curved to short-allantoid, 9–13.5 × 4–6 μ...6. *E. fuliginea*

i. Dikaryophyses nodulose to branching, not becoming filled with brown granules..j.

j. Basidia sphaeropedunculate, clavate, to rarely subglobose, longitudinal septa usually diverging to form enucleate basidial stalks; basidiospores cylindrical-curved to elliptical, 10.5–15 × 4.5–7.5 μ; dikaryophyses terminating in nodulose to branching apices, 1–3.5 μ in diameter.....8. *E. laccata*

j. Basidia subglobose, broadly obovate to pyriform, only rarely with enucleate stalks; basidiospores allantoid, 12–17.5 × 4–6 μ; dikaryophyses little branched to nodulose, 1–3.5 μ in diameter, or less often subcylindrical, 4.5–10 μ in diameter...................................9. *E. grisea*

k. Dikaryophyses of one type, nodulose to little branched, 1.5–4.5 μ in diameter; fertile hyphae thick-walled; subhymenial hyphae thick-walled; basidiospores allantoid, 14–17 × 4.5–5.5 μ..........................14. *E. leucophaea*

k. Dikaryophyses of two types, some nodulose to branching, others subcylindrical to subfusiform, often greater than 5 μ in diameter; fertile hyphae thin-walled; subhymenial hyphae thin- or thick-walled................l.

l. Basidiocarps with conspicuous tubercles due to subhymenial accumulations of mineral granules; subcylindrical dikaryophyses often projecting

above the hymenium; basidiospores elliptical to cylindrical-curved, 9.5–16.5 × 5–7.5 μ . . . . 11. *E. sublivida*

l. Basidiocarps smooth to scattered-tuberculate, sometimes with mineral accumulations piercing the hymenium; cylindrical dikaryophyses rarely projecting beyond the hymenium . . . . m.

m. Arid-waxy; margins effused or abrupt but not reflexed on drying; basal hyphal layer relatively thin . . . . n.

m. Coriaceous; margins abrupt, usually reflexed on drying; basal hyphal layer relatively thick . . . . o.

n. Basidia 10–15 × 8–12.5 μ; basidiospores usually allantoid to cylindrical-curved; 10–14 × 3.5–5.5 μ; known only from tropical and subtropical regions . . . . 10. *E. mucedinea*

n. Basidia 19–27 × 13–17.5 μ; basidiospores cylindrical-curved, 15–22 × 7.5–9.5 μ; known only from temperate regions . . . . 12. *E. calcea*

o. Basidiocarps white to ochraceous; surface tardily becoming scattered-tuberculate; subhymenial hyphae rarely with walls over 1 μ in thickness; basidiospores 10–15 × 5–7.5 μ . . . . 13. *E. macrospora*

o. Basidiocarps ochraceous to vinaceous; surface usually smooth; subhymenial hyphae with walls up to 1.5–2 μ in thickness; basidiospores 10–14.5 × 5–6 μ . . . . 15. *E. alliciens*

ACCEPTED SPECIES

1. EXIDIOPSIS CALOSPORA Bourd. & Galz., Bull. Soc. Mycol. Fr. **39**: 263. 1924. FIG. 1

Sebacina calospora (Bourd. & Galz.) Bourd. & Galz., Hym. Fr. 46. 1928.

Waxy-gelatinous, effused in small patches; drying to an evanescent or grayish, pruinose layer; fructification 15–60 μ thick, consisting of a loosely arranged basal layer of prostrate hyphae, 1.5–4.5 μ in diameter, with clamp-connections throughout, giving rise to the fertile hyphae which are ascending, obliquely ascending, or nearly horizontal; thicker fructifications consisting primarily of irregularly arranged fertile hyphae and collapsed basidia in the lower portions and ascending fertile hyphae and turgid basidia in the upper portions; fertile hyphae 3–5 μ in diameter, with clamp-connections throughout, bearing basidia terminally or on lateral proliferations through the clamp-connections at the base of the older basidia; probasidia at first clavate, becoming obovate, ovate, or subglobose, becoming 2–4-celled by the formation of longitudinal, oblique, or transverse septa, 11–15 × 10–12 μ; epibasidia either not differentiated or if present tubular and abruptly attenuate, then up to 20 μ in length and 2–3.5 μ in diameter; basidiospores arising as fusiform, sigmoid structures with attenuate apices, becoming irregularly forked or developing lateral branches, 17–35 × 2.5–5.5(–7) μ, capable of germinating by repetition.

On dead wood. Known from Ontario, Iowa, and Europe.

Type locality: France.

Illustrations: Bourd. & Galz., Hym. Fr. 46, *f. 23;* Univ. Iowa Stud. Nat. Hist. **13**: 9, *f. 2–6*; Lloydia **4**: 26, *f. 41–43.*

Specimens examined: Iowa: Iowa City, *GWM,* 3 Nov., 1929, *RJB,* 16 May, 1955, *RJB 55–1;* North Liberty, *DPR 549, 2278.*

This species is well characterized by the long, fusiform basidiospores, the irregularly arranged fertile hyphae which are often up to 5 μ in diameter, and the irregular arrangement of the entire fructification. In the specimens examined, it was noted that the fertile hyphae are frequently prostrate or obliquely ascending, with the result that the septa formed in the basidia are often transversely or obliquely arranged. Basidia formed near the surface of the fructification lack differentiated epibasidia, whereas those formed within the basidiocarp have distinct epibasidia of variable length.

2. EXIDIOPSIS PROLIFERA (Rogers) Ervin, Mycologia **49**: 123. 1957. FIG. 2

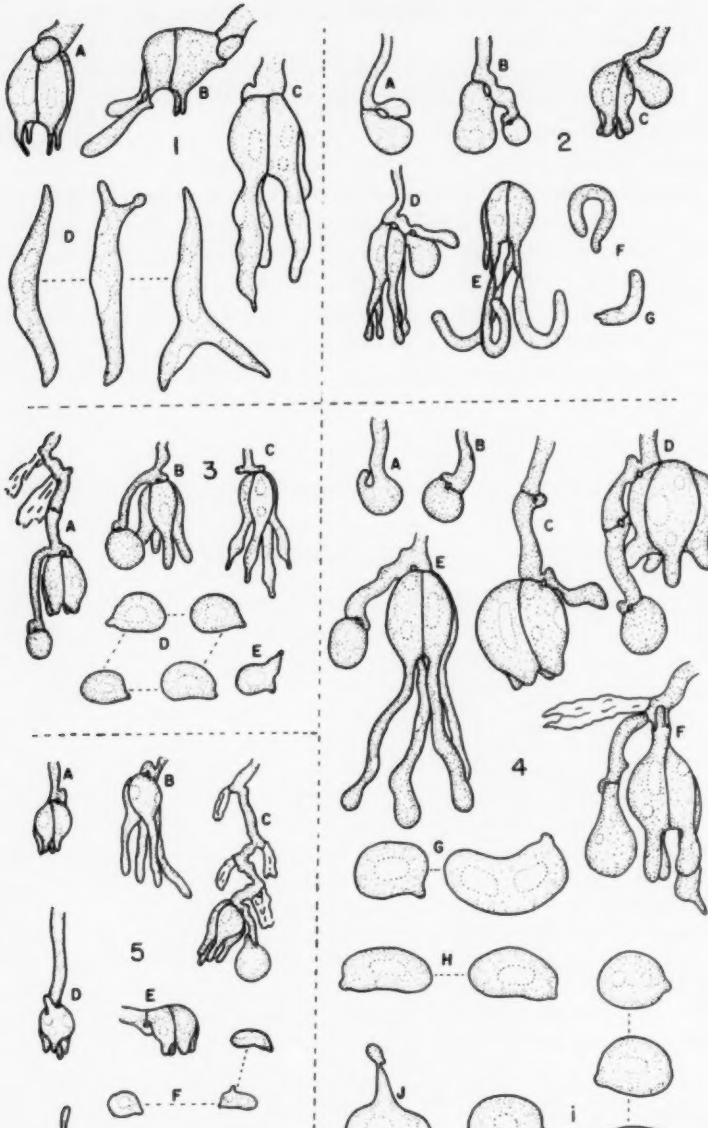
Sebacina prolifera Rogers, Mycologia **28**: 350. 1936.

Mucous-gelatinous, effused, appearing hyaline to grayish-hyaline when fresh; surface pruinose and tuberculate in thicker specimens; margins adnate and indeterminate; drying to a colorless or faint white, pruinose, interrupted layer; fructifications 15–90 μ thick, consisting of an irregularly arranged basal layer of subdistinct hyphae, with clamp-connections throughout, 1.5–2.5 μ in diameter, giving rise to an ascending layer of fertile hyphae bearing a loosely arranged hymenial layer; dikaryophyses apparently not formed; fertile hyphae 2–3.5 μ in diameter, generally enlarged below basidia, proliferating laterally through large, conspicuous, trumpet-shaped clamp-connections to form a close series of basidia; basidia at first subglobose to obovate, becoming oblong to pyriform and 2–4-celled, often guttulate, septa generally longitudinal, 10–14 × 7.5–9(–10) μ; epibasidia tubular, 2–3 μ in diameter at the base, up to 20 μ in length, with long attenuate sterigmata; basidiospores usually guttulate, cylindrical-curved to subhelicoid, blunt to attenuate at basal end, blunt to slightly attenuate at apex, 18–27(–30) × 2.5–4 μ, capable of germinating by repetition.

On dead wood, usually in an advanced stage of decay. Known only from the type locality.

Type locality: Iowa City, Iowa.

Illustrations: Mycologia **28**: 352, *f. 1–33;* 357, *f. 34;* Lloydia **4**: 26, *f. 38–40.*



FIGS. 1–5.

Specimens examined: Iowa: Iowa City, Short Estate (formerly Linder's Woods), *DPR 80* (HOLOTYPE), *DPR 525, 537, KW 214.*

A species well characterized by the mucous-gelatinous texture, the narrow cylindrical-curved to subhelicoid spores, and the lateral proliferations of the fertile hyphae through the conspicuous, trumpet-shaped clamp-connections.

Only one additional collection (*KW 214*) known to me has been identified since McGuire's (**1941**) treatment of this species. This specimen is identical with the other collections with respect to the structure of the fructification and the characters of the fertile hyphae. However, the basidiospores of the latest collection are strongly recurved to nearly helicoid and up to 28 μ in length, whereas the collections by Rogers possess basidiospores which are, at most, cylindrical-curved and the largest is only 20 μ in length. Since basidiospores are present in the most recent collection which approach the size and shape of the spores in the type collection, it seems advisable to include the latest collection within the concept of *E. prolifera.*

As pointed out by Rogers, *E. prolifera* is apparently closely related to *E. calospora,* as indicated by the similarities of the morphology of the spores and basidia and of the structure of the fructifications in the two species.

3. EXIDIOPSIS GLAIRA (Lloyd) Wells, Lloydia **20**: 48. 1957. FIG. 3
Tremella glaira Lloyd, Mycol. Writ. **5**. Mycol. Notes **60**: 874. 1919.
Sebacina opalea Bourd. & Galz., Bull. Soc. Mycol. Fr. **39**: 262. 1924.

Soft-gelatinous, widely effused, pale grayish-hyaline, smooth to undulate; drying to a hyaline or yellowish, vernicose layer, often pruinose, sometimes evanescent; margins indeterminate and adnate; fructifications 20–300 μ thick, consisting of a thin basal layer of distinct hyphae, 1.5–3 μ in diameter, parallel with the substrate, apparently lacking in thinner

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FIGS. 1–5. FIG. 1. *Exidiopsis calospora.* A–C. Basidia, × 875 (A, B from *RJB 55–1;* C from *DPR 549*). D. Basidiospores, × 875 (*DPR 549*). FIG. 2. *Exidiopsis prolifera.* A–E. Basidia, × 875 (*KW 214*). F, G. Basidiospores, × 875 (F from *KW 214;* G from *DPR 525*). FIG. 3. *Exidiopsis glaira.* A–C. Basidia, × 875 (A from *KW 75;* B, C from *KW 53*). D, E. Basidiospores (D from *GWM,* 6 April, 1941, × 1000; E from *KW 75,* × 875). FIG. 4. *Exidiopsis molybdea.* A–F. Basidia, × 875 (A–C from *DPR 86;* D from *DPR 582;* E from *GWM 8877;* F from *DPR 926*). G–J. Basidiospores, × 875 (G from *DPR 86;* H from *DPR 582;* I from *GWM 4635;* J from *DPR 926*). FIG. 5. *Exidiopsis fugacissima.* A–E. Basidia, × 875 (A–D from *DPR 523;* E from *RJB 55–3*). F, G. Basidiospores, × 875 (F from *RJB 55–3;* G from *DPR 523*). All figures drawn with the aid of a camera lucida or a Zeiss drawing apparatus.

fructifications, then an ascending layer of loosely interwoven, subdistinct hyphae, which terminates in a hymenium of fertile hyphae and dikaryophyses; dikaryophyses 1–2 μ in diameter, becoming indistinct, simple to little branched; fertile hyphae tortuous, 1.5–4 μ in diameter, proliferating from the base of the probasidia through or near clamp-connections with conspicuous loops, bearing basidia in a zone 25–70 μ wide; basidia ovate to subglobose, 9–13 × 7–10.5 μ, becoming cruciate-septate or rarely only 2-celled; epibasidia slender, flexuous, often inflated near the apex, up to 45 μ in length, 1.5–2.5 μ in diameter; basidiospores subglobose to obovate, rarely broadly ovate to elliptical, often guttulate, 6–8(–10) × 4–6 μ, capable of germinating by repetition.

On dead wood, usually decorticated. Known from Ontario, New York, Kentucky, North Carolina, Iowa, Sweden, and France.

Type locality: Near Femsjö, Sweden.

Illustrations: Bourd. & Galz., Hym. Fr. 42, *f. 21;* Lloydia **4**: 18, *f. 26–34;* **20**: 47, *f. 2, a–c* (not d); Univ. Iowa Stud. Nat. Hist. **17**: 77, *f. 13;* **19**(**3**): 109, *f. 13.*

Specimens examined: Canada: Ontario, TRT 8501. United States: Kentucky, *KW 75, 77, 78;* Iowa, *GWM 6395,* 6 April, 1941, and several other collections. Sweden: Near Femsjö, C. G. Lloyd Myc. Coll. 27070 (HOLOTYPE, in BPI).

E. glaira is characterized by obovate to subglobose basidia subtended by conspicuous, loop-like clamp-connections and usually obovate to ovate basidiospores with obliquely attached apiculi. This species is apparently closely related to *E. molybdea* and *E. fugacissima;* however, it is readily distinguished from both by the microdimensions and structure of the basidiospores and basidia. Dikaryophyses are lacking in *E. fugacissima,* whereas such structures are present, but often indistinct, in *E. glaira.*

Re-examination of the collections from Brazil (*J. Rick,* May, 1942) and Panamá (*GWM 2655*) indicates that they are not to be included in the concept of this species. Thus the accurate determinations to date indicate that *E. glaira* is restricted to temperate regions.

4. EXIDIOPSIS MOLYBDEA (McGuire) Ervin, Mycologia **49**: 123. 1957. FIG. 4

Sebacina molybdea McGuire, Lloydia **4**: 17. 1941.
Sebacina atra McGuire, Lloydia **4**: 27. 1941.

Mucous to waxy-gelatinous, effused, indeterminate; grayish-hyaline to deep gull gray; surface often pruinose, smooth to undulate or tuberculate; drying evanescent, forming a hyaline film, or an ochraceous to

whitish crust; margins similar and closely adnate; fructifications 50–600(–750) μ thick, consisting of an ascending, interwoven hyphal layer with collapsed basidia dispersed throughout and terminating in the hymenium of turgid basidia and, in most specimens, dikaryophyses, a thin, prostrate layer rarely present; subhymenial hyphae hyaline, tortuous, with clamp-connections throughout, thin-walled or developing a rather thick gelatinous wall in older fructifications, 2.5–5.5 μ in diameter; dikaryophyses sparse, sometimes absent, simple to little branched, becoming early indistinct, 1.5–3.5 μ in diameter, embedded in a gelatinous layer 10–30 μ above the probasidia; fertile hyphae tortuous, forming basidia by proliferation through or near clamp-connections at the base of the probasidia, 2–3.5 μ in diameter; turgid basidia in a dense zone 30–75 μ wide; probasidia arising as obovate or subglobose structures subtended by conspicuous, loop-like clamp-connections, becoming subglobose to obovate and 2–4-celled by the formation of longitudinal, oblique or rarely transverse septa, often guttulate, 11.5–19.5 × 10–16.5 μ; epibasidia tubular and flexuous, up to 70 μ in length and 2–3.5(–4.5) μ in diameter, expanding up to 4.5 μ in diameter at the apex; basidiospores subglobose, elliptical to cylindrical-curved, frequently guttulate, (9–)10.5–19 × 5.5–8.5(–10) μ, germinating directly or by repetition.

On wood, usually in an advanced stage of decay. Known from Vermont, Massachusetts, North Carolina, Georgia, and Iowa.

Type locality: North Liberty, Iowa.

Illustrations: Lloydia **4**: 18, *f. 22–25;* 34, *f. 67–72* (as *S. atra*); Jour. Elisha Mitchell Sci. Soc. **60**: *pl. 6, f. 12–16.*

Specimens examined: Vermont: *E. T. Reese,* 18 June, 1951. Massachusetts: *DPR 926.* Iowa: *DPR 20, 86, 530, 540, 569, 582* (HOLOTYPE of *Sebacina atra* McGuire), *2279, AM and DPR 2316, GWM 4634, 4635, 4664* (HOLOTYPE), *8877, J. M. McGuire,* 26 April, 1939, 9 May, 1940, and several other collections.

McGuire (**1941**) separated *S. atra* and *S. molybdea* on the basis of difference in basidiospore size and shape, 9–13.5 × 6–8.5 μ and broadly ovate in *S. molybdea,* 14–19 × 6–8 μ and cylindrical-curved in *S. atra;* the difference in the shape of the basidia, obovate to subglobose in *S. molybdea,* globose in *S. atra;* and the presence or absence of dikaryophyses, lacking in *S. atra* and present in *S. molybdea.* The description of *S. atra* was based on a single collection; *S. molybdea* was defined from numerous collections, all from eastern Iowa. The morphological characters which McGuire emphasized are distinct in the specimens available at that time; however, these characters appear to be variable in several collections more recently collected or identified. For example, *DPR 86* has subglobose basidia, sparse dikaryophyses, and some spores of the

same size and shape as those in the holotype of *S. atra*. The same is true of *DPR 540*. It is difficult to maintain the distinction between the two species as they are defined by McGuire, especially in view of the fact that the specimens assigned to the two species have similar basidiocarp structure and similar method of basidial development; therefore, they are here treated as synonyms. *S. molybdea* is preferred as the name for this species, since this name has appeared most frequently in the literature.

Olive (**1947**) reports collections of *S. molybdea* lacking clamp-connections at the base of the basidia. I have not noted this feature in any of the specimens examined; in fact, the conspicuous loop-like, sub-basidial clamp-connections are a consistent feature in this species.

5. **Exidiopsis candida** (Olive) Wells, comb. nov. FIG. 6

Tremella sordida Speg., Bol. Acad. Nac. Cordoba **11**: 175. 1887. Not *Exidiopsis sordida* (Olive) Wells, 1957.

Sebacina candida Olive, Bull. Torrey Bot. Club **85**: 21. 1958.

Soft waxy-gelatinous; at first of pure white, radiating tufts of hyphae, then pulvinate and translucent, finally becoming confluent and forming a light grayish-hyaline to cinereous, pruinose layer, attached throughout the lower surface; drying to a hyaline, grayish-pruinose, or fuscous crust; margins at first whitish-fimbriate, then abrupt and sometimes free, often reflexed on drying; surface smooth, undulate to tuberculate; fructifications (100–)225–810 μ in thickness, consisting of a thin, loosely interwoven, prostrate layer, an ascending layer of loosely interwoven hyphae terminating in the hymenium of fertile hyphae and dikaryophyses, growth strata rarely evident; subhymenial hyphae distinct, with elaborate clamp-connections throughout, 1.5–5 μ in diameter, collapsing in older specimens, rarely developing a thickened, gelatinous wall; dikaryophyses simple to little branched, rarely exceeding the probasidial level, sparse, arising from the fertile hyphae, 1–2.5 μ in diameter; subcylindrical dikaryophyses very rarely present, hyaline, up to 40 μ in length, 5–6 μ in diameter; fertile hyphae forming basidia in series or clusters by lateral proliferations through or near the sub-basidial clamp-connections, 1.5–4.5(–6) μ in width; basidia in a dense zone 20–75 μ wide, probasidia arising as clavate or cylindrical structures subtended by well-defined clamp-connections, becoming subglobose, obovate, to pyriform, rarely sphaeropedunculate, sometimes basal stalk delimited by diverging longitudinal septa, apical portion becoming 2–4-celled, (11–)12–25.5 × (9–)10.5–15.5 μ, collapsed basidia often developing a light yellow-granular content; epibasidia tubular, somewhat flexuous, up to 30(–70) μ in length, 3–4.5(–6) μ in diameter; basidiospores short-cylindrical,

broadly elliptical to subglobose, guttulate, (7–)8–12.5(–13.5) × 5–8 μ, capable of germinating by repetition.

On dead wood. Known from Panamá, Colombia, Argentina, Hawaii, and Tahiti.

Type locality: Tahiti.

Illustration: Bull. Torrey Bot. Club **85**: 20, *f. 8*.

Specimens examined: Panamá: Prov. Chiriquí, *GWM 2363*. Colombia: Sierra Nevada de Santa Marta, *GWM 3535*. Argentina: Tierra del Fuego e Isla de los Estados, *Spegazzini 27252* (HOLOTYPE of *Tremella sordida* Speg., in LPS). Hawaii: Oahu, *DPR 1020, 1199, 1244, 1245, 1246, 1247, 1248, 1249, 1250, 1256, 1924*. Tahiti: *L. S. Olive T-442* (HOLOTYPE of *Sebacina candida* Olive, in NY).

This species is characterized by thick fructifications with abrupt margins, well-defined ascending hyphal layer lacking collapsed basidia, subglobose to pyriform basidia which frequently develop a yellow-granular content after spore discharge, and guttulate, usually short-cylindrical basidiospores. The dikaryophyses are very sparse, do not form a distinct layer above the basidia, and appear to arise always from the fertile hyphae. Since the basidia are frequently formed very near the surface, the epibasidia are often short and broad; however, long, flexuous epibasidia arising from deeply embedded basidia are not uncommon.

As is typical of many tropical specimens, the features of the older specimens upon drying are rather obscure. This is true of the type specimen but not of Martin's collections nor of most of Roger's Hawaiian specimens.

The holotype of *Sebacina candida* Olive differs from the remaining specimens assigned to this species only by the thinner basidiocarps. The dikaryophyses, basidia, and basidiospores are essentially similar. The holotype of *Tremella sordida* Speg. also belongs to this species; however, the name can not be transferred to *Exidiopsis* as it would become a later homonym of *Exidiopsis sordida* (Olive) Wells.

6. EXIDIOPSIS FULIGINEA Rick, Brotéria sér. Bot. **5**: 8. 1906.
Sebacina adusta Burt. Ann. Missouri Bot. Gard. **2**: 764. 1915.
Sebacina variseptata Olive, Mycologia **40**: 595. 1948.
Sebacina fuliginea (Rick) Olive, Bull. Torrey Bot. Club **85**: 90 1958.

Waxy to cartilaginous-gelatinous, widely effused, at first hyaline to light yellow, becoming light brown, reddish brown or olive-gray; surface often grayish- or whitish-pruinose, smooth or undulate, usually with

protruding strands of agglutinate, whitish hyphae; margins often lighter, adnate, indeterminate; drying to a yellow, reddish-brown or gray, vernicose layer; fructification 35–375 μ thick, consisting of a basal hyphal layer, ascending hyphal layer which is rarely lacking, and the hymenium; mineral granules often scattered throughout the hymenium and subhymenial regions; basal hyphal layer usually dense, parallel with the substrate, becoming indistinct; ascending hyphal layer at first distinct, loosely interwoven, becoming indistinct, lacking in thinner specimens, hymenium of simple to little branched dikaryophyses, subcylindrical dikaryophyses, and fertile hyphae; simple to little branched dikaryophyses, 1.5–3 μ in diameter, somewhat nodulose, becoming filled with brown granules, disintegrating and leaving the granules scattered throughout the hymenium, granulation less often extending into the subhymenial region; clavate to subcylindrical dikaryophyses often arising from fertile hyphae, hyaline, rarely terminating in finely-branched tips, seldom emergent, 25–45 × 8–10 μ, sometimes absent, fertile hyphae 2.5–4.5 μ in diameter, bearing basidia in dense clusters by lateral proliferations through or near conspicuous clamp-connections; probasidia arising as elongate structures, subtended by clamp-connections; becoming clavate, obovate or ovate, rarely subglobose, often guttulate, becoming 2–4-celled by longitudinal to oblique septa, (9–)10–16.5(–18) × 8.5–12 μ; epibasidia tubular, often flexuous, up to 30 μ in length, 2–3.5 μ in diameter; basidiospores cylindrical and laterally depressed to allantoid, often guttulate, (8–)9–13.5 × (3.5–)4–6(–7) μ, capable of germinating by repetition.

On dead wood, often corticated. Known from Idaho, Florida, Louisiana, Cuba, British Guiana, Colombia, and Brazil.

Lectotype locality: São Leopoldo, Brazil.

Illustrations: Ann. Missouri Bot. Gard. **2**: *pl. 27, f. 19;* Mycologia **40**: 596, *f. 2, 12–27, 34–39;* Lloydia **20**: 47, *f. 5.*

Specimens examined: Idaho: Priest River, *J. R. Weir 12* (HOLOTYPE of *Sebacina adusta* Burt). Florida: Highlands Hammock, *C. L. Shear 714*. Louisiana: St. Martinsville, *A. B. Langlois,* 3 June 1889; *L. S. Olive La. 95* (HOLOTYPE of *Sebacina variseptata* Olive). Cuba: Santa Clara Prov., *W. L. White 432*. British Guiana: Bartica, *D. H. Linder 551*. Panamá: Prov. Chiriquí, *GWM 2501*. Colombia: Sierra Nevada de Santa Marta *GWM 3354*. Brazil: São Leopoldo, *J. Rick,* 1904, *J. Rick,* 1905 (LECTOTYPE), *J. Rick,* 1929, *J. Rick,* 1933, *J. Rick,* 1935 (2 collections), *J. Rick,* 1936, *J. Rick,* 8 March, 1940; Parecy Novo, *J. Rick,* 1938; Rio Grande do Sul, *J. Rick,* Oct., 1939.

E. fuliginea is characterized by the tendency of the fertile hyphae to form dense clusters of basidia by lateral proliferations through or near

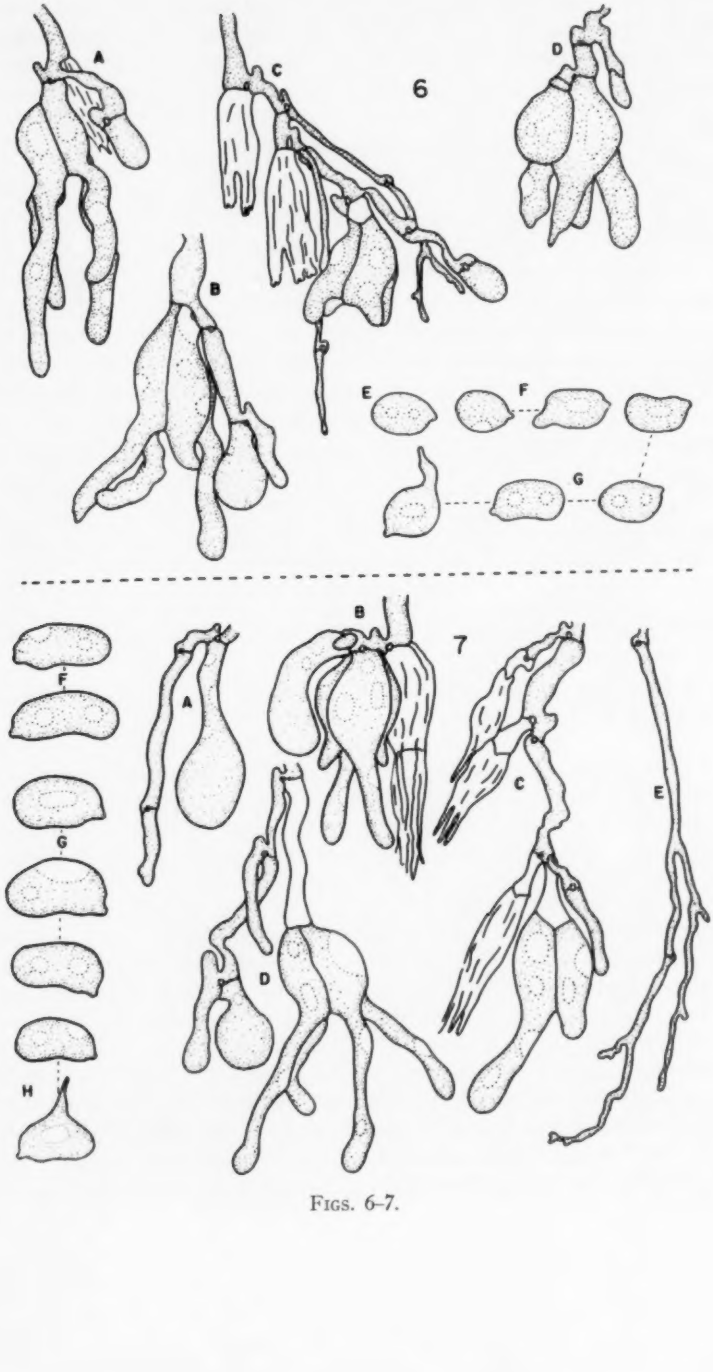
sub-basidial clamp-connections, the allantoid spores, and the slender dikaryophyses which become granular and disintegrate. In some specimens the cylindrical dikaryophyses may form a conspicuous part of the hymenial layer; in others these structures are apparently completely absent.

It does not seem advisable to recognize *Sebacina adusta* as a distinct species since several of the specimens of *E. fuliginea* examined approach the type of *S. adusta* in color and texture. The type of *S. adusta* is apparently a relatively young fructification, as the dikaryophyses have not developed the yellow granules to such an extent as have the majority of the tropical specimens examined. Therefore, the relatively light color of the type of *S. adusta* is apparently due to the small amount of yellow granules in the dikaryophyses. I find the basidia to be quite variable in this species and would not, therefore, separate *S. adusta* from *Exidiopsis fuliginea* merely because the septa in the type of *S. adusta* are usually nearly longitudinal, rather than often oblique, nor because the basidia are obovate to ovate rather than often clavate. The basidia of *E. fuliginea* vary from subglobose to clavate, and the septations vary from longitudinal to nearly transverse. It appears that the orientation of the septa depends on the relative position of the basidia.

7. EXIDIOPSIS FUGACISSIMA (Bourd. & Galz.) Sacc. & Trott. apud Sacc., Syll. Fung. **21**: 452. 1912. FIG. 5

Sebacina fugacissima Bourd. & Galz., Bull. Soc. Mycol. Fr. **25**: 28. 1909.

Mucous-gelatinous, widely effused, hyaline to grayish hyaline or brownish in thicker specimens; surface smooth to undulate; margins indeterminate to completely adnate; on drying evanescent or forming a hyaline to reddish-brown vernicose layer; fructification 20–250 μ in thickness, consisting of a very thin prostrate layer, which is frequently absent, and a loose ascending layer of fertile hyphae terminating in a basidial layer, growth strata sometimes evident in thicker specimens; dikaryophyses sparse to absent, rarely exceeding basidial level, simple to little branched, arising from fertile hyphae, 1–2 μ in diameter; fertile hyphae single strands or branching, 1.5–3 μ in diameter, forming basidia in an acropetal series by lateral proliferations through or near conspicuous loop-like clamp-connections, older specimens revealing flexuous fertile hyphae with the attached, collapsed basidia present at intervals and superficially appearing short-stalked because of the collapse of a portion of the sub-basidial clamp-connections; basidia subglobose to slightly ovate or obovate, becoming 2–4-celled by the formation of oblique to longi-



FIGS. 6–7.

tudinal septa, 5–7.5(–8.5) × 4.5–7 μ; epibasidia tubular, up to 17 μ in length, 1.5–2 μ in diameter; basidiospores cylindrical-curved to obovate, 4.5–7 × (2–)2.5–4 μ, germinating with germination tube or by repetition.

On rotten wood, usually in an advanced stage of decay. Known from North Carolina, Iowa, California and Europe.

Type locality: France.

Illustration: Lloydia **4**: *26, f. 54–57.*

Specimens examined: Iowa: Iowa City, *GWM,* 3 Oct., 1934, *DPR 523, 528, 531, 541, 542, R. J. Bandoni 55–3, KW 90, 148;* E. Okoboji, *DPR 84, 524, 536;* California: Napa Co., *KW 468.*

E. fugacissima is well characterized by the relatively simple structure of the fructification, the "zigzag" appearance of the fertile hyphae of thicker specimens, and the conspicuous, loop-like clamp-connections at the base of the basidia and through or near which the fertile hyphae proliferate. Macroscopically the fructifications of thinner specimens are quite difficult to detect, forming only thin, mucous-gelatinous layers on the under surface of well-rotted logs, whereas thicker specimens form a conspicuous brownish layer. Olive (**1954**) has reported the occurrence of this species in North Carolina.

Essentially the same type of fertile hyphae as in *E. fugacissima* is found in such species as *E. glaira, E. molybdea,* and *E. candida,* to which *E. fugacissima* is probably closely related. The connection between *E. glaira* and *E. fugacissima* appears to be quite close because of the similarity in basidial structure and the relative simplicity of the structure of the fructifications of the two species; however, these two species are easily separated by the difference in sizes of the basidia and basidiospores.

The relationship between *E. fugascissima* and *Sebacina podlachica* and *S. sublilacina* is not, in my opinion, as apparent as has been previously postulated. There is considerable distinction in the structure of the basidia, since both *S. podlachica* and *S. sublilacina* have a basidium which develops an enucleate stalk. There is no such stalk in *E. fugacissima,* since the clamp-connection is present immediately beneath the inflated portion of the subglobose basidium.

FIGS. 6, 7. FIG. 6. *Exidiopsis candida,* × 875. A, B, D. Basidia (A, B from *DPR 1199;* D from *GWM 2363*). C. Portion of fertile hypha with attached dikaryophyses (*DPR 1245*). E–G. Basidiospores (E from *DPR 1245;* F from *GWM 2363;* G from *DPR 1199*). FIG. 7. *Exidiopsis laccata,* × 875. A–D. Basidia (A from *KW 378;* B from *KW 412;* C from *KW 307;* D from *Galzin 15223*). E. Dikaryophysis (*KW 307*). F–H. Basidiospores (F from *Galzin 15287;* G from *KW 412;* H from *KW 378*). All figures drawn with the aid of a camera lucida.

8. **Exidiopsis laccata** (Bourd. & Galz.) E. Robena Luck-Allen, comb. nov. FIG. 7

Sebacina laccata Bourd. & Galz., Bull. Soc. Mycol. Fr. **39**: 262. 1924.

Sebacina mesomorpha Bourd. & Galz., Bull. Soc. Mycol. Fr. **39**: 262. 1924.

Widely effused, indeterminate, waxy-gelatinous, grayish-hyaline to yellowish; surface smooth, undulate, or nearly tuberculate, sometimes pruinose; drying to a hyaline, yellowish, or dark brown vernicose layer, margins adnate, mineral accretions sometimes apparent; fructification 60–720 μ in thickness, growth strata occasionally evident, consisting of a thin prostrate layer, which may be lacking, an ascending layer of branching interwoven, distinct hyphae, 1.5–4 μ in diameter, thin-walled and with clamp-connections throughout, terminating in the hymenium, consisting of dikaryophyses and basidia; dikaryophyses distinct, forming a well-defined layer above the basidia, terminating in narrow, nodulose to branching apices, 1–3.5(–5) μ in diameter; fertile hyphae 2–4.5 μ in diameter, proliferating through or near the distinct, sub-basidial clamp-connections to form basidia in series or in dense clusters; probasidia arising as cylindrical to clavate structures, becoming sphaeropedunculate, clavate, or rarely subglobose, often becoming differentiated into fertile apical portions and enucleate stalks by the diverging longitudinal septa, 15–35 × 9.5–14(–15) μ, stalk when present up to 25 μ in length, 2–4.5 μ in diameter, fertile portion 10.5–22 μ in length and becoming 2–4-celled; epibasidia tubular, usually flexuous, sometimes remaining turgid after the attached hypobasidial segment collapses, up to 60 μ in length and 2.5–4.5 μ in diameter; basidiospores cylindrical-curved to elliptical, usually guttulate, (9–)10.5–15 × 4.5–7.5 μ, capable of germination by repetition.

On dead wood. Known from California, Costa Rica, Colombia, Tahiti, Europe, and North Africa.

Type locality: France.

Illustration: Bourd. & Galz., Hym. Fr. 41, *f. 20*.

Specimens examined: California: *KW 307, 378, 409, 412, 470, 475, 526, 527, 565, 642,* and numerous other collections. Costa Rica: *C. W. Dodge 9169*. Colombia: Hacienda Cincinnati, *GWM 3774*. France: *Galzin 15223* (SYNTYPE of *S. mesomorpha,* in PC), *15287* (SYNTYPE of *S. mesomorpha,* in PC), *15550* (SYNTYPE, in PC), *17802* (SYNTYPE, in PC). Tahiti: *L. S. Olive T-335* (Herb. L. S. Olive).

This species is well characterized by the narrow, usually branching dikaryophyses which form a distinct layer above the nearly mature basidia, the clavate to sphaeropedunculate basidia which, especially in the thicker specimens, become differentiated into fertile apical portions

and enucleate stalks by the diverging longitudinal septa, and the relatively large cylindrical-curved basidiospores.

The morphology of the basidia is quite varied. In the thinner specimens they are obovate to subglobose with the enucleate stalks formed only in a minority of cases, whereas in the thicker specimens the basidia are predominately sphaeropedunculate and only rarely lack the stalks. In addition, the variation in thickness is coupled with the variation in macroscopic aspect. The thinner specimens, upon drying, form a hyaline crust; the thicker specimens dry to a conspicuous dark-brown or nearly black layer.

Neuhoff (**1936**) was apparently the first to suggest that *S. laccata* and *S. mesomorpha* were the same species. Luck-Allen (**1959**) concluded that the two were the same and suggested reducing *S. mesomorpha* to synonymy, since *S. laccata* has page priority. Although Neuhoff treats the species as *S. mesomorpha,* he only suggested that *S. laccata* is the same and did not formally reduce the latter epithet to synonymy; therefore, it seems desirable to follow Luck-Allen's treatment. As both Neuhoff and Luck-Allen suggest, there is no basis on which to separate the two species. The syntypes of *S. laccata* are somewhat thinner in section, with larger basidia and spores than those of the syntypes of *S. mesomorpha;* however, other specimens examined have intermediate characters. The data on the packets of these specimens, which were collected by Galzin and studied by Bourdot, indicate that they were examined prior to the preparation of the original descriptions; therefore, they are considered as syntypes. Holotypes were apparently not designated.

9. EXIDIOPSIS GRISEA (Pers.) Bourd. & Maire, Bull. Soc. Mycol. Fr. **36**: 71. 1920. FIG. 8

Thelephora grisea Pers. Mycol. Eur. **1**: 149. 1822.
Exidiopsis effusa Bref., Unters. **7**: 94. 1888. Nomen nudum.
Thelephora effusa Bref. ex Sacc., Syll. Fung. **6**: 541. 1888.
Exidiopsis quercina Vuill., Bull. Soc. Sci. Nancy II **10**: 30. 1890. Nomen nudum.
Sebacina glauca Pat., Bull. Soc. Mycol. Fr. **9**: 140. 1893.
Thelephora glauca (Pat.) Sacc., Syll. Fung. **11**: 117. 1895.
Exidiopsis effusa (Bref. ex Sacc.) Möll., Protobasid. 82. 1895.
Sebacina quercina Vuill. ex R. Maire, Bull. Soc. Mycol. Fr. **18**: suppl. 66. 1902.
Sebacina effusa (Bref. ex Sacc.) R. Maire, Bull. Soc. Mycol. Fr. **18**: suppl. 67. 1902.

Sebacina grisea (Pers.) Bres., Ann. Mycol. **6**: 45. 1908.
Sebacina peritricha Bourd. & Galz., Bull. Soc. Mycol. Fr. **25**: 26. 1909.
Exidiopsis peritricha (Bourd. & Galz.) Sacc. & Trott. apud Sacc., Syll. Fung. **21**: 452. 1912.
Sebacina plumbea Bres. & Torr., Brotéria sér. Bot. **11**: 87. 1913.
Sebacina plumbea Burt, Ann. Missouri Bot. Gard. **2**: 765. 1915. Not *Sebacina plumbea* Bres. & Torr., 1913.
Sebacina plumbescens Burt, Ann. Missouri Bot. Gard. **3**: 241. 1916.
Sebacina burti Trott. apud Sacc., Syll. Fung. **23**: 573. 1925.
Sebacina uvida (Fries) Bres. subsp. *peritricha* (Bourd. & Galz.) Bourd. & Galz., Hym. Fr. 44. 1928.[5]
Sebacina umbrina Rogers, Univ. Iowa Stud. Nat. Hist. **17**: 39. 1935.
Exidiopsis plumbescens (Burt) Wells, Lloydia **20**: 53. 1957.

Waxy-gelatinous, at first effused in small patches which become confluent to form fructifications up to several centimeters in the longer dimension, grayish hyaline, surface usually strongly pruinose under the lens; margins at first fibrillose and adnate, becoming abrupt in older specimens; drying to a hyaline, white, light gray, or bluish-gray vernicose layer or crust, often with a vinaceous tint; fructifications 50–750 μ in thickness, consisting of a basal hyphal layer, an ascending layer, and the hymenium; basal layer thin, of hyphae loosely arranged, parallel with the substrate, tortuous, with clamp-connections throughout, hyaline and thin-walled, 2–5(–6.5) μ in diameter; ascending layer of loosely arranged, toruloid, distinct hyphae, with clamp-connections throughout, 1.5–4 μ in diameter, sometimes inflated up to 6 μ in diameter, thin-walled, usually with collapsed basidia and cylindrical dikaryophyses dispersed throughout; hymenium of fertile hyphae, branching dikaryophyses and often cylindrical dikaryophyses; small mineral accumulations usually scattered throughout the fructification; branching dikaryophyses tortuous, short branched, nodulose, becoming indistinct, forming a layer 10–35 μ above the septate basidia, 1–3.5(–4.5) μ in diameter; subcylindrical dikaryophyses absent to abundant, hyaline, apparently arising from the fertile hyphae, rarely septate with clamp-connections, becoming flexuous, subcylindrical, subclavate, to subfusiform, (18–)20–90(–150) × 4.5–10 μ; fertile hyphae tortuous, 2.5–5 μ in diameter, forming basidia in an acropetal series by lateral proliferations through or near rather conspicu-

[5] At the time of the first publication of this name, Bourdot and Galzin were apparently convinced that this was a distinct species; however, in 1928 they indicated that they considered it a subspecies by printing the name in slanted type. The other subspecies, *Sebacina uvida* (Fries) Bres. subsp. *uvida*, which was automatically proposed in their later publication, does not apply to *E. grisea*.

ous sub-basidial clamp-connections; turgid basidia in a zone 35–75 μ wide; probasidia arising as obovate to elongate structures, becoming subglobose, broadly obovate to ovate or pyriform, becoming 2–4-celled by the formation of longitudinal or oblique septa, 11–21 × 8–12(–13.5) μ; epibasidia tubular, often somewhat flexuous, up to 60 μ in length and 2–3.5 μ in diameter; basidiospores allantoid, usually conspicuously guttulate, (11–)12–17.5 × (3.5–)4–6 μ, capable of germinating by repetition.

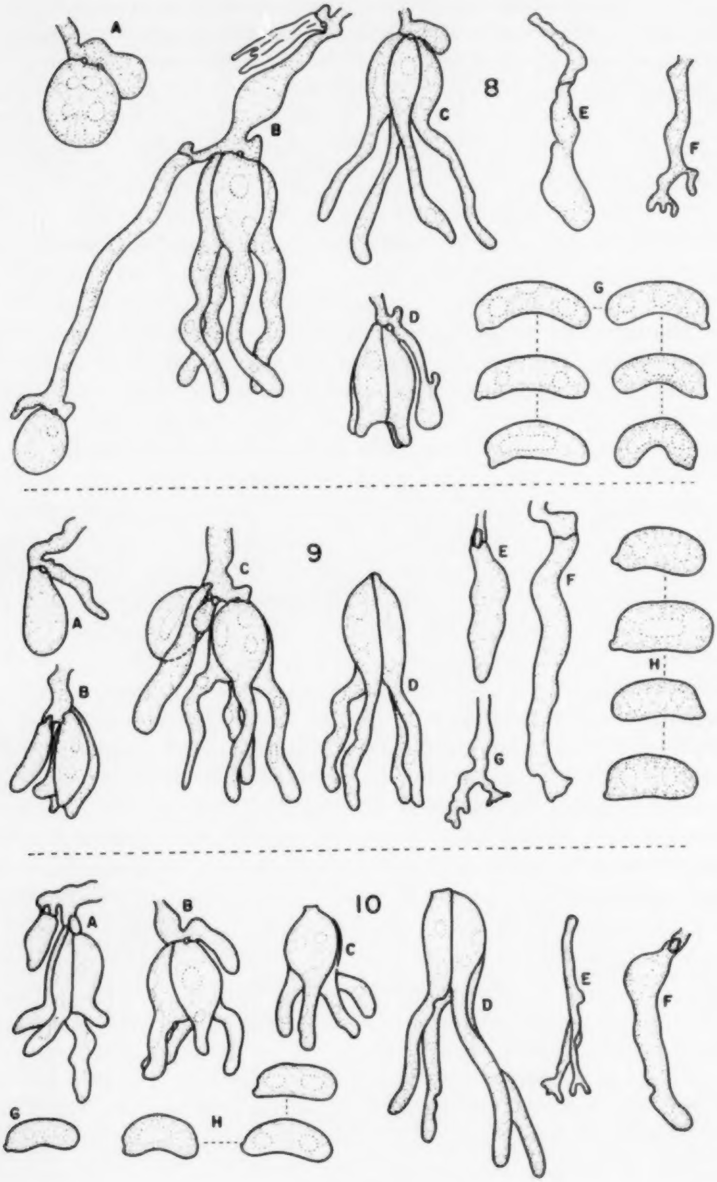
On wood, often corticated. Known from Nova Scotia, Ontario, British Columbia, Oregon, California, Iowa, Ecuador, Hawaii, and Europe.

Type locality: Europe.

Illustrations: Brefeld, Unters. **7**: *pl. 5, f. 20–22;* Bull. Soc. Mycol. Fr. **18**: suppl. *pl. 1, f. 5–15;* Brotéria sér. Bot. **11**: 87, *f. 8;* Ann. Missouri Bot. Gard. **2**: 765, *f. 6;* Univ. Iowa Stud. Nat. Hist. **17**: 35, *f. 19;* Lloydia **4**: 26, *f. 50–53, 75–79;* **20**: 55, *f. 6;* Mycologia **39**: 102, *f. 8;* Friesia **4**: 92, *f. 4*; Dansk Bot. Arkiv **19**: 21, *f. 13,* 31, *f. 23, 24.*

Specimens examined: Canada: Nova Scotia, *K. A. Harrison,* 4 April, 1953; Ontario, TRT 16832, 16838; British Columbia, *RJB BC-136, 313, 367, 460, 512, IK & RJB BC-139.* United States: Iowa, *DPR 278* (HOLOTYPE of *Sebacina umbrina* Rogers); Washington, MICH 13068, *W. N. Suksdorf,* 18 Nov., 1902 (HOLOTYPE of *Sebacina plumbescens* Burt, in FH); Oregon, *DPR 570, 571, 1124, 1125;* California, *W. B. Cooke 16577, KW 226, 396, 466, 473, 479, 481, 498, 505, 506, 508, 541, 542, 555, 566, 577, 601, 612,* and numerous other specimens. Ecuador: Pichincha, *Lagerheim,* March, 1892 (LECTOTYPE of *Sebacina glauca* Pat., in FH). Hawaii: Oahu, *DPR 1920.* Sweden: *J. A. Nannfeldt 9312, 10021, 13284; S. Lundell,* 4 Nov., 1935, *981, 1416* (BPI), *2040; S. Lundell & M. A. Donk 3798.* Denmark: *M. P. Christiansen 2599.* Austria: Tirol, *V. Litschauer 34.* Italy: *J. Bresadola,* 1902 [determined by Bresadola as *Sebacina uvida* (Fries) Bres.]. France: *L. Maire,* Sept., 1919 (BPI), Jan., 1924 (BPI); Fraize, 3 Oct., 1918 (FH); Herb. J. Bresadola, 24 April, 1900 [NEOTYPE, determined by Bresadola as *Sebacina grisea* (Pers.) Bres., in S]; *Galzin 2106* (PC), *2011, 6485* (the latter two are authentic specimens of *Sebacina peritricha* Bourd. & Galz., in PC). Portugal: *C. Torrend 366* (HOLOTYPE of *Sebacina plumbea* Bres. & Torr., in S).

E. grisea is characterized by narrow, allantoid, guttulate basidiospores, subglobose to broadly obovate basidia subtended by rather conspicuous clamp-connections, and slender, branching dikaryophyses and, in some collections, subcylindrical dikaryophyses. The rather long list of synonyms is most probably due to the wide variation in the appearance



FIGS. 8–10.

and color exhibited by the fructifications at different ages and under different environmental conditions. As the species is interpreted here, the macroscopic aspect varies from a hyaline or light-gray bloom to a dark gray or vinaceous-gray fructification. Only in the thicker specimens is the macroscopic aspect of any aid in determination. As in the case of *E. fuliginea,* the presence or absence of cylindrical dikaryophyses is considered as a variable feature and has, therefore, not been used to separate the group into two taxa.

E. grisea appears to be related to *E. calcea* and *E. alliciens,* since these species exhibit similar types of dikaryophyses and the basidiospores and basidia differ only in dimensions and shape. With respect to texture and characters of the fertile hyphae, *E. grisea* is similar to *E. sordida, E. laccata,* and, to a lesser extent, *E. molybdea.*

The earliest valid name for this species appears to be *Thelophora grisea* Pers., published in 1822. A portion of an authentic specimen from Bresadola labeled *Sebacina grisea* (Pers.) Bres. from the Naturhistoriska Riksmuseum has been examined and agrees with Persoon's description macroscopically. I have assumed that Bresadola's interpretation is correct in this case; therefore, this specimen is designated as the neotype of *Thelophora grisea* Pers.

Another specific epithet which has frequently been applied to this species is derived from *Thelephora viscosa β uvida* Fries (**1828**); however, since this name clearly refers to a taxon of subspecific rank, "*uvida*" was not validated as a specific epithet until 1838 (Fries, **1838**), when the combination *Corticium uvidum* Fries was proposed. Lundell (in Lundell and Nannfeldt, **1947**) states that *C. uvidum* is a synonym of *Corticium lividum* (Pers. ex Fries) Fries; therefore, *C. uvidum* probably does not apply to this species at all.

Vuillemin published the combination "*Exidiopsis quercina* Vuill." prior to the establishment of *Exidiopsis* as a genus. The specific epithet was subsequently validated by R. Maire. Bourdot and Galzin (**1928**)

FIGS. 8–10. FIG. 8. *Exidiopsis grisea,* × 875. A–D. Basidia (A, C from *Christiansen 2599;* B from *KW 226;* D from *Litschauer 34*). E. Subcylindrical dikaryophysis (*Nannfeldt 9312*). F. Branching dikaryophysis (*Litschauer 34*). G. Basidiopsores (*KW 555*). FIG. 9. *Exidiopsis sublivida,* × 875. A–D. Basidia (A, B from holotype; C, D from *J. Rick,* 1933). E–G. Dikaryophyses (E, G from holotype; F from *J. Rick,* 1930). H. Basidiospores (*J. Rick,* 1930). FIG. 10. *Exidiopsis macrospora,* × 875. A–D. Basidia (A, C from *Stevenson & Davidson,* 19 Aug., 1939; B from Bourdot; D from *GWM,* 21 July, 1941). E, F. Dikaryophyses (*Stevenson & Davidson,* 19 Aug., 1939). G, H. Basidiospores (G from *Stevenson & Davidson,* 19 Aug., 1939; H from *GWM,* 21 July, 1941). All figures drawn with the aid of a camera lucida.

list *"Exidiopsis effusa"* and *"Exidiopsis quercina"* as synonyms of *Sebacina uvida* (Fries) Bres. Brefeld's treatment of the subgenus *Exidiopsis* and his description of the species tend to confirm the synonymy listed by Bourdot and Galzin; however, it is difficult to correlate Brefeld's measurements with the dimensions of the basidia and basidiospores as determined in the present study. Nevertheless, Brefeld states that *"Exidia effusa"* perhaps has been identified earlier as *Corticium uvidum.*

The two authentic specimens of *Sebacina peritricha* Bourd. & Galz. differ only slightly from specimens determined by Bresadola as *S. grisea* and *S. uvida;* therefore, I have included *S. peritricha* in the list of synonyms. Bourdot and Galzin (**1928**) in their discussion of *Sebacina uvida* subsp. *peritricha* state that they consider it as intermediate between *S. grisea* and *S. uvida.*

The collection of *Sebacina glauca* Pat. here designated as the lectotype forms a grayish-white crust over the substrate. The internal structure and microdimensions indicate that the specimen should be included within the concept of this species.

The holotype of *Sebacina plumbea* Bres. & Torr. (*Torrend 366*) is, in my opinion, to be included within the concept of *Exidiopsis grisea.* It is only somewhat thicker than the usual collection.

The internal structure of *Sebacina plumbescens* Burt is identical with the other specimens assigned to this species. The cylindrical dikaryophyses are not as apparent in this specimen as in some other specimens, since the collection is in rather poor condition.

10. EXIDIOPSIS MUCEDINEA (Pat.) Wells, Lloydia **20**: 46. 1957.
Sebacina mucedinea Pat., Bull. Herb. Boiss. **3**: 60. 1895.
Thelephora mucedinea (Pat.) Sacc., Syll. Fung. **14**: 214. 1899.
Exidiopsis manihoticola Viégas, Bragantia **3**: 23. 1943.

Arid-waxy, effused, in the thicker portions appearing arachnoid to pruinose, white, light gray to pale buff, often with scattered, mineral tubercles piercing the hymenium; margins thinning out, usually pruinose and somewhat lighter; drying to a thin, white, light-gray or ochraceous-buff layer; fructifications 20–130 μ thick, composed of a thin basal layer of indistinct hyphae parallel with the substrate, an intermediate layer of distinct, branching, interwoven, ascending hyphae, 1.5–3.5 μ in diameter, sometimes lacking in thinner fructifications, and a hymenial layer, 20–50 μ wide, of fertile hyphae and simple to little branched, nodulose dikaryophyses, 2.5–4 μ in diameter, intergrading to cylindrical dikaryophyses, up to 13.5 μ in diameter; branching dikaryophyses sometimes disintegrating and imparting a light yellowish-granular appearance to

the upper portion of the hymenium; mineral granules scattered throughout the fructification; probasidia formed by proliferations through or near inconspicuous clamp-connections at the base of the older basidia, becoming obovate to subglobose and 2–4-celled by the formation of longitudinal septa, 10–15(–17) × 8–12.5 μ; epibasidia tubular, often somewhat tortuous, up to 18 μ in length, 2.5–3 μ in diameter, each becoming tipped with a short subulate sterigma, basidiospores allantoid, often strongly curved, or elliptical and laterally depressed, granular to guttulate, 10–14(–16) × 3.5–5.5(–6.5) μ, germinating by repetition or directly.

On dead wood. Known from Brazil, Ecuador, Panamá, and Tahiti.

Type locality: Pululahuana, Ecuador.

Illustrations: Lloydia **7**: *69, f. 4;* Bragantia **3**: 25–26, *f. 1–5;* Lloydia **20**: 47, *f. 1;* Bull. Torrey Bot. Club **85**: 6, *f. 1F,* 25, *f. 10.*

Specimens examined: Panamá: Canal Zone, *GWM 2018, 4080, 6159.* Brazil: São Leopoldo, *J. Rick,* 1935; Parecy, *J. Rick,* 1935; Salvador, *J. Rick,* 13 June, 1943; São Paulo, IACM 3203, 3689 (HOLOTYPE of *Exidiopsis manihoticola* Viégas). Tahiti: *L. S. Olive T-178, T-259* (NY).

A species well characterized by the usually strongly curved basidiospores, the intermediate hyphal layer composed of branching, interwoven hyphae, and the thin fructifications usually appearing white, gray, or light buff and strongly pruinose.

Olive (**1958**) has pointed out the presence of cylindrical dikaryophyses in this species. Such structures are difficult to detect in dried specimens.

11. **Exidiopsis sublivida** (Pat.) Wells, comb. nov. FIG. 9

Heterochaete sublivida Pat., Bull. Soc. Mycol. Fr. **24**: 2. 1908.

Arid-waxy, effused, sordid-hyaline; surface smooth to tuberculate, tubercles usually somewhat lighter; margins adnate, indeterminate, somewhat lighter; drying to an ochraceous-buff or reddish-brown layer; fructification (20–)40–310 μ in thickness, consisting of a thin basal layer of subdistinct hyphae, 1.5–4.5 μ in diameter, thin-walled, with clamp-connections throughout, terminating in a hymenium of slender, branching dikaryophyses, subcylindrical dikaryophyses, and fertile hyphae; mineral accumulations scattered throughout the fructifications; macroscopically visible tubercles due to accumulation of mineral granules in certain areas, the hymenium in some cases interrupted by these accumulations, hymenium in other cases continuous; subcylindrical dikaryophyses arising mainly from the fertile hyphae, subtended by clamp-connections, also subfusiform or subclavate, hyaline, sometimes projecting above the hymenium, 20–80 × 3.5–10.5 μ; slender dikaryophyses simple to little

branched, somewhat nodulose near apices, sparse, 1.5–3.5 μ in diameter; fertile hyphae flexuous, forming basidia in clusters by lateral proliferations through or near the sub-basidial clamp-connections, 2–4.5 μ in diameter; probasidia arising as elongate or cylindrical structures, then becoming clavate to obovate or ovate, developing 1–3 longitudinal septa, 13.5–22.5 × 7.5–11 μ; epibasidia somewhat flexuous, tubular and tipped with subulate sterigmata, up to 21 μ in length, 3–4.5 μ in diameter; basidiospores elliptical and laterally depressed to cylindrical-curved, 9.5–16.5(–18.5) × 5–7.5 μ, germinating directly or by repetition.

On rotten wood. Known from Louisiana and Brazil.

Type locality: St. Martinville, Louisiana.

Specimens examined: Louisiana: St. Martinville, *A. B. Langlois,* 18 Oct., 1897 (HOLOTYPE, in FH). Brazil: São Leopoldo, *J. Rick,* 1930, *J. Rick,* 1933; Parecy, *J. Rick,* 1935 (2 collections).

Bodman (**1952**) in her treatment of the genus *Heterochaete* excluded *Heterochaete sublivida,* since the tuberculate surface of the type collection is due to an accumulation of mineral granules. In some cases the hymenium is interrupted, in other cases the basidial layer is continuous over the tubercle.

Microscopically the species is somewhat similar to *E. macrospora,* since both species possess subcylindrical dikaryophyses and have a similar basidial structure, and in both species there is present a basal, prostrate hyphal layer. In *E. sublivida* the subcylindrical dikaryophyses may project above the hymenium; however, it does not seem desirable to term these structures "cystidia" since they apparently originate from the same hyphae as the structures which do not project above the surface. The surface of *E. macrospora* may become tuberculate but not to such an extent as the specimens of *E. sublivida.*

The specimen collected by Rick in São Leopoldo in 1930 is similar to the other specimens examined except it is quite thin and the basidia are consistently 2-celled.

12. **Exidiopsis calcea** (Pers.) Wells, comb. nov. FIG. 11

Thelephora acerina var. *abietis* Fries, Syst. Mycol. **1**: 453. 1821.

Thelephora calcea Pers., Mycol. Eur. **1**: 153. 1822.

Thelephora calcea c. *albido-fuscescens* Fries, Elench. Fung. **1**: 215. 1828.

Corticium calceum (Pers.) Fries, Epicr. Syst. Mycol. 562. 1838, p.p.

Xerocarpus farinellus Karst., Bidrag Finska Vet.-Soc. **37**: 139. 1882.

Sebacina letendreana Pat., Rev. de Mycol. **7**: 152. 1885.

Thelephora letendreana (Pat.) Sacc., Syll. Fung. **6**: 541. 1888.

Sebacina calcea (Pers.) Bres., Fungi Trid. **2**: 64. 1892.
Corticium abietis (Fries) Romell, Bot. Not. **1895**: 72. 1895.

Arid-waxy, adnate, arising in small patches which become confluent to form an irregular crust with somewhat abrupt margins, grayish-white to ochraceous-tawny; surface pruinose; margins somewhat lighter; drying to a dingy pulverulent layer; fructification 50–200 μ thick, consisting of a thin basal layer of hyphae parallel with the substrate, 1.5–3 μ in diameter, hyaline, with clamp-connections throughout, becoming indistinct, and an ascending layer terminating in the fertile hyphae and dikaryophyses; mineral accretions often present in the subhymenial regions, numerous brownish mineral granules in vicinity of dikaryophyses and frequently attached to them; dikaryophyses of two types, one type cylindrical to clavate, arising from the fertile hyphae, frequently septate with clamp-connections, up to 50 μ in length and 2–7 μ in diameter, and the other type simple to little branched, arising from the basal hyphal layer, tortuous, becoming indistinct, 0.5–2.5 μ in diameter, forming a layer 35–75 μ above the mature basidia; fertile hyphae tortuous, 2–4(–5.5) μ in diameter, bearing basidia in clusters by proliferations through or near clamp-connections at the base of the probasidia; probasidia at first elongate, becoming obovate to ovate, 2–4-celled at maturity, guttulate, 19–27(–35) × (12–)13–17.5 μ; epibasidia tubular, up to 85 μ in length 3–4 μ in width; basidiospores cylindrical-curved to suballantoid, granular to guttulate, 15–22 × (6–)7.5–9.5 μ, germinating directly or by repetition.

On living limbs or on dead corticate or decorticate wood. Known from Manitoba, Saskatchewan, North Central United States, and Europe.

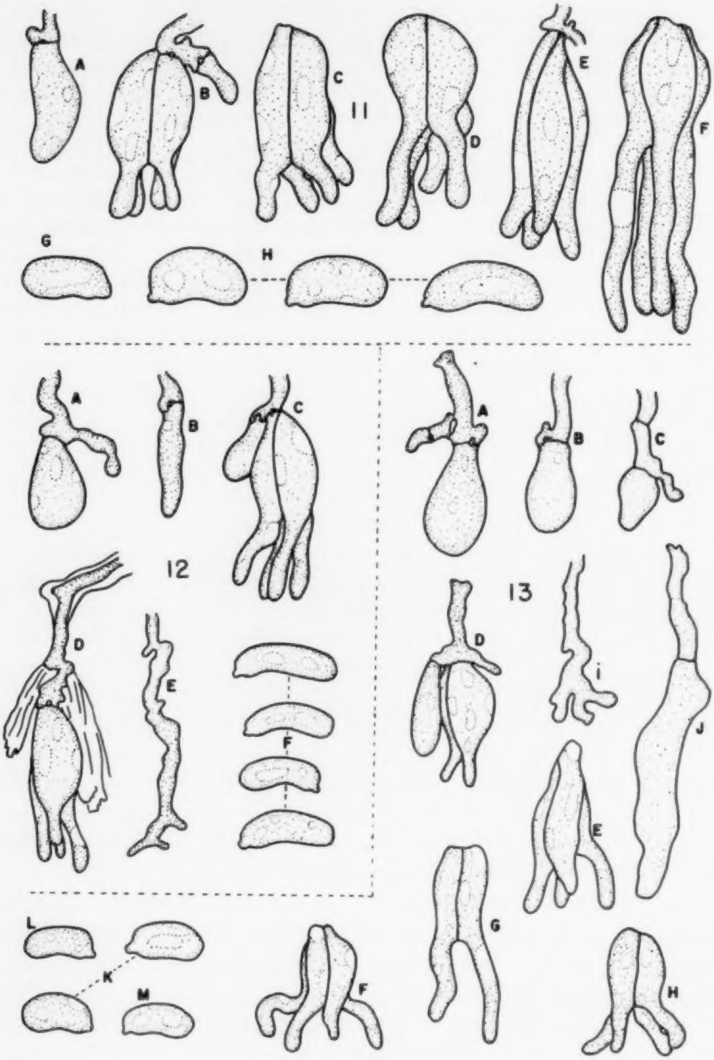
Type locality: Europe.

Illustrations: Lloydia **4**: 15, *f. 5, 6,* 26, *f. 46–49;* Univ. Iowa Stud. Nat. Hist. **17**: *pl. 20, f. 1–23, pl. 21, f. 24–37.*

Specimens examined: Illinois: Milan, *E. B. Wittlake 87.* Iowa: *GWM 1506, DPR 548,* and two other collections.

This species is characterized by large, guttulate basidia and basidiospores, two types of dikaryophyses, and the fact that the entire hymenium has a yellowish tint when stained with Phloxine and Congo Red.

This species is apparently closely related to *E. macrospora* as indicated by its arid-waxy texture, the two types of dikaryophyses, and the similarity in form of the fertile hyphae, basidia, and basidiospores to those of *E. macrospora.* The margins of *E. calcea* are abrupt at maturity, whereas the margins of *E. macrospora* are abrupt and frequently reflexed especially after the specimen has dried. In addition, the basidia and basidiospores of *E. macrospora* are distinctly smaller than those of *E. calcea.*



FIGS. 11–13.

FIGS. 11–13. FIG. 11. *Exidiopsis calcea*, × 875. A–F. Basidia (A, B, F from *GWM 1506;* C, D, E from *DPR 548*). G, H. Basidiospores (G from *GWM 1506;* H from *GWM*, 13 Aug., 1936). FIG. 12. *Exidiopsis leucophaea*, × 875. A–C. Basidia (Lloyd Myc. Coll. 46411). D. Portion of fertile hypha showing develop-

McGuire (**1941**) discusses the application of the specific epithet of this species. Malençon (**1954**) reports the presence of *Sebacina calcea* in France and describes a new variety; i.e., *Sebacina calcea* (Pers.) Bres. var. *corticoides* Malençon; however, his description and illustrations suggest *E. macrospora* rather than *E. calcea,* as here defined.

13. **Exidiopsis macrospora** (Ell. & Everh.) Wells, comb. nov. FIG. 10

Corticium macrosporum Ell. & Everh., Bull. Torrey Bot. Club **27**: 49. 1900. Not *Corticium macrosporum* Bres. 1908.

Sebacina macrospora (Ell. & Everh.) Burt, Ann. Missouri Bot. Gard. **2**: 759. 1915.

? *Sebacina monticola* Burt, Ann. Missouri Bot. Gard. **2**: 761. 1915.

Eichleriella macrospora (Ell. & Everh.) Martin, Univ. Iowa Stud. Nat. Hist. **18**(3): 48. 1944.

Coriaceous, arid, at first thin, in scattered patches, and with adnate, fimbriate margins, becoming confluent, thicker and with abrupt margins which may become reflexed upon drying; at first pale drab or ochraceous, becoming white with ochraceous patches to chalk-white; surface at first smooth, often finely pruinose at lower magnifications, becoming scattered-tuberculate; drying to an ochraceous to shining white layer; fructification (25–)60–300(–550) μ in section, consists of a basal layer of hyphae, becoming yellowish and somewhat thick-walled, with clamp-connections throughout, 2.5–4 μ in diameter, either parallel with the substrate or interwoven and ascending, and an ascending interwoven layer of indistinct toruloid hyphae with clamp-connections throughout, 2.5–4(–6) μ in diameter, terminating in the hymenium; hymenium composed of fertile hyphae, slender dikaryophyses, and subcylindrical, septate dikaryophyses; mineral granules usually abundant throughout, often very abundant in the vicinity of the hymenium; cylindrical dikaryophyses apparently arising from the fertile hyphae, sometimes clavate or subfusiform, flexuous, hyaline, 35–70 × 3.5–10 μ; slender dikaryophyses simple to little branched, usually nodulose, becoming indistinct, 1.5–4(–5) μ in diameter, forming a well-defined layer 20–75 μ wide above the mature basidia; fertile hyphae toruloid, 2–5 μ in diameter, forming basidia in clusters

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ment of thickened wall (holotype). E. Dikaryophysis (holotype). F. Basidiospores (Lloyd Myc. Coll. 46411). FIG. 13. *Exidiopsis alliciens,* × 875. A–H. Basidia (A from *W. A. & E. L. Murrill,* 14–15 Dec., 1908; B from *J. Rick,* 1932; C, D from *J. Rick,* 1936; E, H from *R. Singer,* 1 Nov., 1942; F from *J. Rick,* 1924; G from *J. Rick,* 1903). I, J. Dikaryophyses (I from *R. Singer,* 1 Nov., 1942; J from *J. Rick,* 1936). K–M. Basidiospores (K from *W. A. & E. L. Murrill* 399; L from *R. Singer,* 1 Nov., 1942; M from *J. Rick,* 1924). All figures drawn with the aid of a camera lucida.

by lateral proliferations through or near sub-basidial clamp-connections; probasidia arising as elongate structures subtended by clamp-connections, becoming ovate, obovate or almost subglobose and developing 2 or 4 longitudinal septa, guttulate, 15–22 × 8–14 μ; epibasidia tubular, often somewhat flexuous, 2–4(–5) μ in diameter, up to 75 μ in length; basidiospores usually cylindrical-curved, guttulate, 10–15(–17) × 5–7.5(–8) μ, germinating by formation of germination tube or by repetition.

On dead wood or bark attached to tree. Known from Ontario, Nova Scotia, Eastern United States, Ohio, Iowa, Missouri, Texas, and Europe.

Type locality: Ohio.

Illustrations: Univ. Iowa Stud. Nat. Hist. **18**(3): 76, *pl. 2, f. 14;* **19**(3): 109, *f. 14,* 113, *f. 36.* Bothalia **7**: 181, *f. 2.*

Specimens examined: Canada: Nova Scotia, *K. A. Harrison,* 26 Oct., 1953. United States: New Hampshire, *H. H. York & L. O. Overholts,* 8 July, 1918; New York, *C. H. Peck* (date unknown); Ohio, *C. G. Lloyd 3113* (HOLOTYPE); Tennessee, *J. A. Stevenson & R. W. Davidson,* 19 Aug., 1939; Florida, Gainesville, *W. A. Murrill,* 14 Aug., 1944; Iowa, 6 collections; Texas, *C. L. Shear,* 7 March, 1904. Denmark: *M. P. Christiansen 609.* Austria: Volders, *M. Rousseau,* Oct., 1910. France: H. Bourdot (date unknown).

This species is distinguished by the often chalk-white fructifications with abrupt margins and the tuberculate surface of most older specimens. Microscopically the obovate basidia and cylindrical-curved basidiospores and the two types of dikaryophyses separate *E. macrospora* from related species.

Olive (**1958**) suggests that this species might be more at home in *Heterochaete.* However, since the hyphal pegs in *E. macrospora* are only weakly developed and do not arise from the subhymenial hyphal regions, the species seems more related to the other species in the genus *Exidiopsis.*

McGuire (**1941**) discussed the possible synonymy of *Sebacina monticola* Burt with this species and concluded that it is difficult to be certain of the nature of the type of *S. monticola,* but that it is probably to be included in *E. macrospora.*

A specimen collected by Rick in Brazil in 1936 has been tentatively identified as *E. macrospora.* However, since I have been unable to find any basidiospores and since the specimen is in poor condition, it does not seem advisable to record this species as occuring in Brazil.

14. **Exidiopsis leucophaea** (Bres.) Wells, comb. nov. FIG. 12

Eichleriella leucophaea Bres., Ann. Mycol. **1**: 116. 1903.

Hirneolina leucophaea (Bres.) Bres. apud Sacc., Syll. Fung. **17**: 209. 1905.

Eichleriella schrenkii Burt, Ann. Missouri Bot. Gard. **2**: 744. 1915.

Hirneolina schrenkii (Burt) Sacc. & Trott. apud Sacc., Syll. Fung. **23**: 575. 1925.

Soft-coriaceous, arising in small patches which may become confluent to form a fructification several centimeters in length; margins abrupt, strongly recurved on drying and then appearing brownish-tomentose; surface smooth and pruinose under the lens, on drying often splitting; drying to an ochraceous to light-gray, brittle crust, often with a vinaceous tinge, sometimes fading to a light buff; fructification 75–750 μ in thickness, consisting of a basal hyphal layer, an intermediate layer, and the hymenium; basal hyphal layer composed of ochraceous, distinct hyphae often arranged in strands, with walls up to 1.5–2 μ in thickness, interwoven, with clamp-connections throughout, 3–5 μ in diameter; intermediate layer of hyaline, thick-walled hyphae arranged parallel with the substrate and ascending in the upper region or ascending from the basal hyphal layer, 2–5 μ in diameter, toruloid; hymenium composed of slender dikaryophyses and fertile hyphae; small mineral granules often abundant in the vicinity of the hymenium; dikaryophyses nodulose to short branched, becoming indistinct, 1.5–4.5 μ in diameter, forming a layer 15–35 μ above the septate basidia; fertile hyphae 2.5–4.5 μ in diameter, toruloid, becoming thick-walled, forming basidia in clusters by lateral proliferation near or through the sub-basidial clamp-connections; probasidia arising as cylindrical to obovate structures, becoming obovate, clavate, or irregular in shape, becoming 2–4-celled by the formation of longitudinal to oblique septa, 15–28(–32) × 8.5–12.5(–14) μ; epibasidia tubular, often quite flexuous, usually enlarging near the apex, up to 35 μ in length, 2.5–3.5 μ in diameter; basidiospores allantoid, usually guttulate, 14–17(–20) × 4.5–5(–6.5) μ, germinating directly or by repetition.

On dead wood, often corticated. Known from Texas, Poland, and France.

Type locality: Poland.

Illustrations: Ann. Mycol. **1**: *tab. 3, f. 2;* Ann. Missouri Bot. Gard. **2**: *pl. 27, f. 8.*

Specimens examined: Texas: *H. von Schrenk,* 9 Feb., 1914 (HOLOTYPE of *Eichleriella schrenkii* Burt). Poland: Ex Herb. J. Bresadola 19 (HOLOTYPE, in S), Ex. Herb. J. Bresadola 1864 (NY). France: Allier, *Galzin 9356* (C. G. Lloyd Myc. Coll. 46411, in BPI).

This species is characterized by the ochraceous, thick-walled subhymenial hyphae with the fertile hyphae soon becoming thick-walled, the allantoid and guttulate basidiospores, and the cupulate aspect of the

fructifications when dry. The brown tomentose margin of the dried specimen is apparently due to exposure of the basal hyphae of the strongly reflexed margin.

E. leucophaea appears to be related to *E. alliciens* and *E. grisea.* The basidia and basidiospores indicate a relationship with *E. grisea,* from which it may be separated by the presence of thick-walled, subhymenial hyphae and the lack of subcylindrical dikaryophyses in *E. leucophaea.* In addition there is considerable difference in the macroscopic aspect of the two species. The internal structure of the fructifications of *E. leucophaea* is similar to that of *E. alliciens;* however, there is a clear distinction in the basidiospores and basidia. In addition, the subcylindrical dikaryophyses present in *E. alliciens* are lacking in *E. leucophaea.*

Bresadola describes the basidiospores as becoming 1–3-septate; however, this has not been observed in the specimens examined during the present study.

The type collection of *Eichleriella schrenkii* Burt is similar in all respects to the specimens referred by Bresadola to *E. leucophaea.*

The collection in the Bresadola Herbarium of the Naturhistoriska Riksmuseum in Stockholm is almost certainly the type collection of this species although not specifically designated as such. This is indicated by the fact that the specimen is described as having been collected on "*Carpini Betuli*" in the month of November both on the packet and in the original description.

15. **Exidiopsis alliciens** (Berk. & Cke.) Wells, comb. nov. FIG. 13

Stereum alliciens Berk. & Cke., Jour. Linn. Soc. Bot. **15**: 389. 1876.
Eichleriella incarnata Bres., Ann. Mycol. **1**: 116. 1903.
Hirneolina incarnata (Bres.) Bres. apud Sacc., Syll. Fung. **17**: 208. 1905.
Eichleriella alliciens (Berk. & Cke.) Burt, Ann. Missouri Bot. Gard. **2**: 746. 1915.
Hirneolina crocata Pat., Bull. Soc. Mycol. Fr. **40**: 31. 1924.
Eichleriella mexicana Burt, Ann. Missouri Bot. Gard. **13**: 334. 1926.
Hirneolina ubatubensis Viégas, Bragantia **5**: 242. 1945.

Coriaceous, arising as small, resupinate patches, becoming confluent and forming fructifications several centimeters in dimension with abrupt margins, ochraceous-buff to vinaceous, sometimes fading to nearly white; margins somewhat lighter, or if reflexed on drying, then brownish tomentose; surface usually smooth and pruinose, rarely with faint concentric zonations; drying somewhat lighter; fructification (100–)200–700(–1000) μ thick, consisting of a basal layer of thick-walled, distinct,

interwoven hyphae, ochraceous, often arranged in strands, with clamp-connections throughout, 2.5–5.5 μ in diameter, an intermediate layer of distinct hyphae which are interwoven, obliquely ascending or arranged parallel with the substrate, with clamp-connections throughout, becoming ochraceous and thick-walled in the lower portion, 2–5 μ in diameter, terminating in the hymenium of dikaryophyses and fertile hyphae; mineral accretions often scattered throughout the fructification; dikaryophyses of two types, one type subcylindrical, subfusiform, or subclavate, hyaline, flexuous, 20–100(–120) μ in length, 3.5–12 μ in diameter, sparse to abundant, the other type simple to little branched, hyaline, thin-walled, sometimes guttulate, becoming indistinct, 1.5–3.5 μ in diameter, forming a layer 10–30 μ above the septate basidia; fertile hyphae flexuous, 3–5 μ in diameter, forming a zone of basidia 25–50 μ wide by proliferations through or near clamp-connections at the base of the probasidia; basidia arising as clavate structures, becoming delimited into 2–4 units by the formation of longitudinal septa, finally obovate, ovate, or rarely elongate, guttulate, (12–)18.5–24(–25) × (7.5–)8.5–12(–13.5) μ; epibasidia often divergent and flexuous, tubular and enlarging towards the apex, 2–4 μ in diameter and up to 40 μ in length; spores cylindrical-curved, often guttulate, 10–14.5 × (4–)5–6 μ, germinating by formation of germination tube or by repetition.

On dead wood which is often still attached. Known from Florida, Mexico, Cuba, British Guiana, Jamaica, Brazil, Poland, and Indo-China.

Type locality: Brazil, San Antonio da boa vista, Rio Javary.

Illustrations: Ann. Missouri Bot. Gard. **2**: *pl. 27, f. 10;* Bragantia **5**: 250, *pl. 6.* Ann. Mycol. **1**: *tab. 3, f. 1.*

Specimens examined: North America: Florida, *W. A. Murrill,* March, 1923 (Ex Missouri Bot. Gard. Herb. 62131), *R. Singer,* 1 Nov., 1942. Mexico: *W. A. & E. L. Murrill 399* (HOLOTYPE of *Eichleriella mexicana* Burt). Cuba: Santa Clara Prov., *W. L. White 563;* Pinar del Rio Prov., *Earle & Murrill,* 8–10 March, 1905 (NY). British Guiana: Georgetown, *D. H. Linder 230.* Jamaica: Castletown Gardens, *W. A. & E. L. Murrill,* 14–15 Dec., 1908 (NY). Brazil: *J. Rick,* 1921 (BPI); São Leopoldo, *J. Rick,* 1929, *J. Rick,* 1930 (BPI); *J. Rick,* 1935, *J. Rick,* 1939; Sta. Maria, *J. Rick,* 1935, *J. Rick* 1936; São Sebastiano, *J. Rick,* March, 1923 (NY); Parecy Novo, *J. Rick,* 1903, *J. Rick,* 1918 (J. S. Weir 14410), *J. Rick,* 1924, *J. Rick,* 1928; São Paulo, *A. S. Costa,* 9 April, 1936 (HOLOTYPE of *Hirneolina ubatubensis* Viégas). Poland: Herb. J. Bresadola 4, 36 (PARATYPES of *Eichleriella incarnata* Bres., in S). Indo-China: Hanöi, *M. Petelot,* 1921 (2 collections, one, *Petelot 45,* the HOLOTYPE of *Hirneolina crocata* Pat., in NY).

This species is characterized by the coriaceous texture of the resupi-

nate, vinaceous to buff basidiocarps with abrupt margins. Although I have not examined fresh specimens of this species, it would appear that the margins are never reflexed when fresh but only upon drying. In the latter state, the margins may appear brownish-tomentose because of the exposure of the basal layer of colored, thick-walled hyphae. The presence of subcylindrical dikaryophyses and the thick-walled basal hyphae are consistent microscopic characters.

Superficially *E. alliciens* appears somewhat similar to *Eichleriella leveilliana* (Berk. & Curt.) Burt; however, the latter species has applanate margins, thickened hyphae throughout the basidiocarps, and no subcylindrical dikaryophyses. In addition, the basidiospores of *Eichleriella leveilliana* are consistently larger than those of *E. alliciens.*

The two specimens of *Eichleriella incarnata* Bres. from Bresadola's Herbarium in the Naturhistoriska Riksmuseum are to be included within the concept of this species. Although the specimens are not in the best of condition, the internal structure and the character of the basidia and basidiospores are similar to the other specimens which have been assigned to this species. Bresadola describes the basidiospores as developing one to three septa, a character which I have been unable to observe in Bresadola's specimens or in the remaining specimens assigned to this species. The two specimens are almost certainly paratypes of the species since the measurements of basidia and basidiospores designated on the packets coincide with the measurements of these structures included by Bresadola in the original description of *E. incarnata.* In addition, the substrates as indicated on the packets are reproduced in the original description.

SPECIES DUBIA

1. *Eichleriella chinensis* Pilát, Ann. Mycol. **38**: 62. 1940.

Apparently Pilát was somewhat doubtful as to the nature of this species, since he was unable to distinguish the basidia and spores. I have been unable to examine any of the three specimens cited in the original description. These specimens were collected in Jehol (Chengtehfu), Chihli Prov., China.

2. *Sebacina dendroidea* (Berk. & Curt.) Lloyd, Mycol. Writ. **4**. Mycol. Notes **39**: 538. 1915.
   Hymenochaete dendroidea Berk. & Curt., Jour. Linn. Soc. Bot. **14**: 69. 1873.

A specimen which Lloyd labeled with his combination consists of a brown mass of hyphae radiating from a central point on the undersurface

of *Ganoderma applanatum* (Pers. ex Fries) Pat. Microscopically it consists of the brown spinose spores of *G. applanatum*, relatively thin-walled, septate hyphae without clamp-connections, and an assortment of hyaline one- or two-celled spores.

Certainly the specimen examined is not a species of *Exidiopsis* or *Sebacina*, and judging from Lloyd's account, the specimens studied by Berkeley do not belong in this group. Subsequently, Lloyd (**1920**) suggested that an older name is *Institale bombacina* Fries and stated, "it has since been proven that it is not a *Sebacina*."

Specimen examined: New York: *W. H. Ballou* (C. G. Lloyd 34091, in BPI).

3. *Exidiopsis moelleri* Rick, Egatea **18**: 344. 1933.

A very small fragment of a specimen labeled by Rick as this species was sent to Professor G. W. Martin. Although the specimen is in poor condition and is too small to permit a generic determination, it is possible to state that it is a resupinate or near-resupinate tremellaceous species. The basidia are subglobose to obovate and 11–14 × 7–10.5 μ, and the basidiospores are cylindrical-curved and 9–10 × 4–5 μ.

Specimen examined: Brazil: *J. Rick*, 5 Sept., 1931.

4. *Sebacina reticulata* Pat., Bull. Herb. Boiss. **3**: 59. 1895.
Thelephora reticulata (Pat.) Sacc., Syll. Fung. **14**: 214. 1899.

I have been unable to locate the type specimen which was collected on dead wood in Ecuador. The original description is strongly suggestive of a species of *Protomerulius* Möll.

5. *Sebacina rufochracea* Höhn. apud Petch, Ann. Rev. Bot. Gard. Peradeniya **9**: 314. 1925.

It has not been possible to examine the type specimen which was collected in Ceylon. The original description is suggestive of *Exidiopsis alliciens*.

6. *Exidiopsis sordida* (Olive) Wells, Lloydia **20**: 51. 1957.
Sebacina sordida Olive, Jour. Elisha Mitchell Sci. Soc. **60**: 21. 1944. Nomen nudum.

The holotype and paratype of this species were examined. Both specimens were apparently very mature when collected, as shown by the

numerous collapsed basidia in the subhymenial region and the indistinct dikaryophyses. Both specimens are infected with a dematiaceous fungus.

The basidia of the holotype are ovate to obovate and 9–11.5 × 8–9 μ, and the cylindrical-curved basidiospores are 10.5–12 × 4–5 μ. This specimen is very similar to those which have been referred to *Exidiopsis grisea;* however, the basidia and spores are smaller than in most specimens. My original (Wells, **1957**) concept of this species was erroneous. The specimens referred to this species at that time have been re-examined and determined as *E. grisea* or *E. candida*. Because of the similarity of the type of *E. sordida* to *E. grisea* and because of the poor condition of the type specimens, it is desirable, I think, to treat *E. sordida* as a dubious member of the genus *Exidiopsis*.

Olive's original description of this species was not accompanied by a Latin description as required by Article 34 of the Intern. Code Bot. Nomenclature, 1956 and, therefore, was not validly published at this time. The original description was an effective publication in accordance with Articles 29 and 31. My transfer of the name to *Exidiopsis* inadvertently resulted in the valid publication of the species name. Since my combination was not the name of a new taxon, Article 34 is not applicable here. Article 32 is pertinent; and since my combination was effectively published in accordance with Articles 29 and 31 and was accompanied by a "reference . . . to a previously and effectively published description . . . ," *Exidiopsis sordida* (Olive) Wells is the only correct name for the taxon.

Specimens examined: North Carolina, *L. S. Olive,* 27 December, 1943 (HOLOTYPE, in NCU), 13 March, 1944 (PARATYPE, in NCU).

7. *Sebacina tenuis* Olive, Bull. Torrey Bot. Club **85**: 21. 1958.

I was unable to locate any distinct tremellaceous basidia in the type. There are obovate to clavate structures visible which are of the dimensions of the basidia as described by Olive; however, I did not see any septations.

Specimen examined: Tahiti: *L. S. Olive T-348* (HOLOTYPE, in NY).

8. *Sebacina tuberculosa* Torrend, Brotéria sér. Bot. **11**: 88. 1913.

I have not been able to examine authentic or type specimens of this species. The specimens on which the original description is based were collected in Portugal. The description is suggestive of *Sebacina podlachica* Bres. or *Sebacina sublilacina* Martin.

SPECIES EXCLUDENDAE

1. *Sebacina alutacea* Wakef., Bull. Misc. Inf. Kew **1922**: 162. 1922.

The single specimen upon which the original description is based incrusts the base of a woody plant, *Shorea robusta* Gaertn. The texture of the fungus is coriaceous and the color varies from light to dark buff. Sections of the specimen reveal a basal layer of prostrate, distinct hyphae terminating in the hymenium. The hymenium is composed of simple to little branched dikaryophyses forming a distinct layer above the ovate, cruciately-septate basidia. The basidia are 14–17 × 8.5–11 μ. Clamp-connections are absent throughout the fructification. Several irregular, thick-walled structures were observed in the hymenium. The specimen, in my opinion, represents one of the numerous variations of *Sebacina helvelloides* (Schw.) Burt and should, therefore, be included within the concept of the latter species.

Specimen examined: India: Madras, *A. F. Minchin*, 26 August, 1918 (HOLOTYPE, in K).

2. *Sebacina bresadolae* Lloyd, Mycol. Writ. **7**. Mycol. Notes **75**: 1362. 1925.

The description and illustration presented by Lloyd indicate that the species should be referred to *Tremellodendron* Atk. Lloyd suggests that it is similar to the species referred by Atkinson to the latter genus.

3. *Sebacina caesia* (Pers. ex Fries) Tul., Jour. Linn. Soc. Bot. **13**: 37. 1871.

Thelephora caesia Pers., Syn. Meth. Fung. 579. 1801.

Thelephora caesia Pers. ex Fries, Syst. Mycol. **1**: 449. 1821.

Sebacina laciniata subsp. *caesia* (Pers. ex Fries) Bourd. & Galz. Hym. Fr. 41. 1928.

The nature of this species is a mystery. Tulasne states that it is closely related to *Sebacina incrustans*, but unlike the latter species the basidiocarps do not incrust the bases of living trees or shrubs or develop erect projections. Pearson (**1920**) suggests that *Tremella epigaea* Berk. & Br. (≡ *Sebacina epigaea*) is the same as *S. caesia* and *Sebacina ambigua* Bres. Apparently, according to Pearson, *S. ambigua* has frequently been applied to the form on wood and *S. caesia* to the form on soil. Bourdot and Galzin indicate that the hyphae lack clamp-connections, and that the basidiocarps may occur on bare soil, incrusting the

bases of living trees, or on prostrate timber. The description by Bourdot and Galzin suggests a close relationship to *S. epigaea.* Christiansen (**1959**) reports the species from Denmark, stating that it is a widely effused, soft-gelatinous form which occurs on soil.

Although I have not seen any authentic specimens of this species, the treatments by various authors strongly suggest that the species is not a member of the genus *Exidiopsis.*

4. *Sebacina crozalsii* Bourd. & Galz., Hym. Fr. 38. 1928.

The collection data on the packets of the two specimens examined suggest that they are the specimens on which the original description was based; i.e., syntypes. These specimens are, in section, composed of a basal layer of thick-walled hyphae, which gives rise to an ascending, agglutinate layer bearing the hymenium of fertile hyphae and simple to little branched dikaryophyses. Clamp-connections are visible on all hyphal elements which are distinct. The basidia are sphaeropedunculate, become separated into fertile apical portions and basal stalks, and are subtended by clamp-connections. The fertile portions of the basidia are 8–10.5 × 7–9 μ, and the basidiospores are cylindrical-curved and measure 7.5–11 × 3.5–5 μ.

These two collections are only thickened forms of *Sebacina podlachica* Bres. The species should, therefore, be reduced to synonymy with Bresadola's species. As McGuire (**1941**) pointed out in his discussion and description of *S. podlachica,* color and thickness are highly variable in this species, whereas the microscopic features are quite characteristic.

Specimens examined: France: *A. de Crozals 23* (SYNTYPE, H. Bourdot 40132, in PC), *38* (SYNTYPE, H. Bourdot 39065, in PC).

5. *Eichleriella gelatinosa* Murrill apud Burt, Ann. Missouri Bot. Gard. **2**: 748. 1915.
Hirneolina gelatinosa (Murrill) Sacc. & Trott. apud Sacc., Syll. Fung. **23**: 575. 1925.

The portion of the holotype examined revealed little concerning the nature of the species. However, the characters of a specimen from Florida, together with the notes of Dr. A. L. Welden on this collection, indicate that the species is not a member of the genus *Exidiopsis.* The basidiocarp is not resupinate nor even near-resupinate; rather it is infundibuliform. The gelatinous hymenium occupies the outer inferior portion, whereas the inner portion is spongy and sterile and is composed

of thick-walled hyphae in an irregular arrangement. The portions of the basidia becoming longitudinally septate are 15–20 × 10–12 μ. The basidiospores are obovate and laterally depressed and 7.5–11 × 5.5–8 μ.

The species does not, in my opinion, belong to any well-described genus.

Specimens examined: Florida: Dade Co., *K. Lampe & A. L. Welden,* 10 Sept., 1957. Jamaica: *W. A. Murrill & W. Harris, Fungi of Jamaica 1087* (HOLOTYPE, in NY).

6. *Sebacina gloeofilum* Olive, Bull. Torrey Bot. Club **85**: 22. 1958.

As is frequently the case with tropical specimens, the features of the holotype of this species are not distinct in mounts prepared from the dried specimen. Nevertheless, I should consider the specimen as belonging to, or closely related to, either *Sebacina podlachica* Bres. or *Sebacina sublilacina* Martin. The basidiospores are somewhat broader than those of most temperate specimens of *S. sublilacina,* but there are indications of hyaline, subulate cystidia characteristic of the latter species. Certainly the specimen should not be included in *Exidiopsis* because of the sphaeropedunculate basidia and the agglutinate hyphae of the dried specimen.

Specimen examined: Tahiti: *L. S. Olive T-120* (HOLOTYPE, in NY).

7. *Sebacina hirneoloides* Pat., Bull. Soc. Mycol. Fr. **9**: 141. 1893.
Thelephora hirneoloides (Pat.) Sacc., Syll. Fung. **11**: 117. 1895.
Hirneolina hirneoloides (Pat.) Sacc. & Trott., Syll. Fung. **19**: 870. 1910.

This species is well characterized by the large, 20–35 × 8–12 μ, subglobose to ovate basidia and the large, 12–22 × 9–15 μ, cylindrical to broadly obovate basidiospores. The basidiocarps are firm-gelatinous to nearly cartilaginous with abrupt margins.

Although hyphal pegs are sparse in the holotype, such structures are more apparent in other specimens, which, I think, belong to the same species. Thus the species should be referred to *Heterochaete* rather than to *Exidiopsis.* I hope to treat this species in greater detail at a later date; however, I now suggest that the correct name is *Heterochaete tremellispora* (Möll.) Bodman (see Bodman, **1952**).

Specimens examined: Ecuador, *G. de Lagerheim,* June, 1892 (HOLOTYPE, in NY). Brazil: Sta Maria, *J. Rick,* 1935 (IA 1534 and one other collection); *J. Rick,* 1936 (IA 1535 and one other collection).

8. *Eichleriella leveilliana* (Berk. & Curt.) Burt, Ann. Missouri Bot. Gard. **2**: 744. 1915.

Corticium leveillianum Berk. & Curt., Hooker's Jour. Bot. & Kew Gard. Misc. **1**: 238. 1849.

Stereum leveillianum (Berk. & Curt.) Berk. & Curt., Grevillea **1**: 163. 1873.

This well-defined species does not appear to be closely related to any species here included in *Exidiopsis*. In texture and macroscopic aspect it approaches *Exidiopsis alliciens;* however, microscopically the two species are very distinct. In *Eichleriella leveilliana* the subhymenial hyphae and dikaryophyses are thick-walled and without clamp-connections and appear similar to the binding hyphae of many of the Polyporales. The only thin-walled hyphae bearing clamp-connections are the fertile hyphae. In *E. leveilliana* the basidiocarps are applanate, and concentric zonations usually are apparent on the hymenial surface. In my opinion, the applanate basidiocarps and thick-walled hyphae without clamp-connections preclude the inclusion of this species in *Exidiopsis*. The species does not, in my opinion, belong to any well-defined genus.

The obovate basidia are (12.5–)13.5–17.5(–18.5) × 8.5–12 μ, and the cylindrical-curved spores are (13.5–)15–19 × (5–)5.5–7.5 μ. The thick-walled, dichotomously-branching dikaryophyses with attenuate apices are distinctive.

Specimens examined: Alabama: Herb. L. M. Underwood, Nov., 1895 (NY), May, 1896 (NY); *Earle & Baker,* 14 April, 1898 (NY). South Carolina: Herb. J. B. Ellis 1759 (NY). Florida: Herb. J. B. Ellis, Jan., 1882 (NY). Bahama Islands: New Providence, N. Y. Bot. Gard. Explor. Bahamas 9713 (NY), 9717 (NY). Cuba: *W. L. White 483.* Jamaica: *W. A. & E. L. Murrill 493.* Brazil: Montenegro, *J. Rick,* 1928 (NY); São Paulo, *H. P. Krug,* 19 Oct., 1940. Argentina: *Digilio & Grassi 595.*

9. *Sebacina microbasidia* Christiansen & Hauerslev, Dansk Bot. Arkiv **19**: 30. 1959.

This species has minute, pustular, soft-gelatinous basidiocarps, which in some regions tend to be confluent and effused. No ascending hyphal layer or dikaryophyses were seen. The basidia are oval to subglobose or rarely obovate and become 2-celled at maturity. They are 6.5–9 × 6–7 μ. There are no sub-basidial clamp-connections nor were any clamp-connections seen on any of the hyphae. The basidiospores are cylindrical-curved and 7–8 × 3.5–4.5 μ.

S. microbasidia is apparently closely related to *Exidia rolleyi* Olive (**1958**). The structure of the basidiocarps and the morphology of the basidia and basidiospores are similar in both species. Since the sizes of basidia and spores as given by Olive and my own measurements of *E. rolleyi* are consistently larger than those of *S. microbasidia,* it is not desirable at this time to equate the two species.

Specimens examined: Denmark: Halskov ved Korsor, K. Hauerslev, 19·IV·57 (HOLOTYPE, in C).

10. *Sebacina podlachica* Bres., Ann. Mycol. **1**: 117. 1903.

Although I earlier (Wells, **1957**) treated this species as a member of the genus *Exidiopsis,* I am now convinced that the sphaeropedunculate basidia and other characters of *S. podlachica* indicate that the species is more closely related to *S. sublilacina, Exidia nucleata, Stypella minor,* etc., than to the species included in *Exidiopsis.*

Additional specimens examined: Oregon, Corvallis, *DPR 539.*

11. *Eichleriella pulvinata* Coker, Jour. Elisha Mitchell Sci. Soc. **43**: 236. 1928.

The type of this species is waxy and pulvinate and varies in color from hyaline to grayish-hyaline. The subhymenium lacks a basal hyphal layer, being composed of a zone of hyphae arising directly from the substrate and terminating in the fertile hyphae and dikaryophyses, the latter being of essentially the same diameter. Because of the form of the basidiocarps and because the basal hyphae lack the thickened wall and ochraceous tint found in the thicker species of *Exidiopsis,* it appears desirable to exclude this species from the genus *Exidiopsis.* It seems more closely related to *Exidia.*

Specimen examined: North Carolina: Chapel Hill, *W. C. Coker,* 4 June, 1922 (HOLOTYPE).

12. *Sebacina sphaerospora* Bourd. & Galz., Bull. Soc. Mycol. Fr. **39**: 263. 1924.

Two specimens determined by H. Bourdot and the specimens deposited in the Mycological Herbarium at the State University of Iowa, which were reported by McGuire (**1941**) as *S. sphaerospora,* were examined. All show a tuberculate structure in cross section, at least in certain portions of the fructifications. There is present in each specimen a basal layer of agglutinate hyphae, ascending in the upper portions

to terminate in the hymenium of sphaeropedunculate basidia and dikaryophyses. Since the dikaryophyses are so completely agglutinate, it is impossible in all cases to record their structure accurately; however, where discernible, they are cylindrical to clavate and 1.5–3.5 μ in diameter.

Martin (**1934b**), in his discussion of the genus *Stypella,* points out that *Stypella minor* Möll. varies from scattered clusters of separate papillae to phases in which the papillae are so densely massed and anastomosed that they form an almost continuous layer. In my opinion, the specimens determined by Bourdot and by McGuire as *S. sphaerospora* represent the nearly confluent phase of *Stypella minor.* The basidia, which were distinct, in the specimens examined are sphaeropedunculate, and become separated into a fertile, apical portion and a basal stalk. The fertile portion varies in diameter from 7–9 μ. The basidia as described and illustrated by Martin (**1943b**) for *Stypella minor* are nearly identical in size and structure. Further the basidiospores in the specimens referred to *S. sphaerospora* are nearly identical in size and shape to the basidiospores of *Stypella minor* as described by Martin.

Since the specimens examined have a tuberculate macroscopic aspect and are of the same texture and color as specimens referred to *Stypella minor* by Martin, they should be referred to that species.

Specimens examined: Ontario: Bear Island, *R. Biggs,* 29 August, 1935. Massachusetts: *AM & DPR,* 16 Nov., 1936. Iowa: several collections. Oregon: *DPR 573, 574, 575.* France: l'Aveyron, *Galzin 6765* (PC), *6791* (PC).

13. *Eichleriella spinulosa* (Berk. & Curt.) Burt, Ann. Missouri Bot. Gard. **2**: 747. 1915.
 Radulum spinulosum Berk. & Curt., Grevillea **1**: 146. 1873.
 Radulum deglubens Berk. & Br., Ann. Mag. Nat. Hist. IV. **15**: 32. 1875.
 Radulum kmetii Bres., Att. Accad. Sci. Lett. Art. Agiati III. **3**: 102. 1897.

The large clavate basidia, which appear to become separated into a fertile apical portion and a basal stalk by the diverging longitudinal septa, and the hyphal spines, which are sometimes partly fertile and which project from the hymenium, preclude the transfer of this species to *Exidiopsis.* To my knowledge, there has not been a critical study of basidial development of this species or of any closely related species; therefore, the exact method of septa formation is not established. It is

my impression that there is a divergence of the longitudinal septa to form the basal stalk such as Rogers (**1947**) has described for *Bourdotia petiolata* (Rogers) Wells; however, Reid (**1956, 1957**) apparently feels that a fertile apical portion, which he considers "the basidium," is separated from a basal stalk by a secondary septum. I should not consider, as suggested by Reid (**1956**), the basidia of *E. spinulosa* as being of the same type as either *Sebacina podlachica* Bres., which has sphaeropedunculate basidia, or *Sebacina umbrina* Rogers (= *Exidiopsis grisea*). The basidia of the latter species only rarely form a sterile stalk. Reid (**1956**) further compares the basidia of *Exidiopsis prolifera* with those of the species of *Pseudotremellodendron* Reid, stating that they are "rather similar." It should be noted, however, that the "broadened subbasidial cell" to which Rogers (**1936**) refers in his discussion of basidial development of *E. prolifera* is a part of the fertile hyphae, and is not homologous to the basidial stalk formed by *Eichleriella spinulosa, Sebacina podlachica,* or by the species of *Pseudotremellodendron.* The basidia of both *Exidiopsis prolifera* and *Eichleriella spinulosa* have basal clamp-connections. The basic difference between the two species is that the basidia of *Eichleriella spinulosa* form basal stalks whereas those of *Exidiopsis prolifera* do not. Development of additional basidia, in both cases, takes place from or near the clamp-connections at the base of the basidia.

This difference in the interpretation of the basidium very probably accounts for the considerable differences in the measurements of these structures obtained by several investigators. My measurements of the entire basidium were 30–60 × (10–)11.5–14.5 μ, whereas those of Reid's (**1957**) are considerably less. Measurements of only the fertile apical portion (the portion which Reid terms the "basidium") were 27–42.5 × 12–13.5 μ, with stalks of 7–21 × 2–4 μ. My measurements of the allantoid basidiospores were (12.5–)16–21 × (5–)7–9 μ.

Since I did not note any significant difference between European and American specimens as did Reid (**1957**), I do not see any necessity of recognizing *Eichleriella deglubans* (Berk. & Br.) Lloyd as a distinct species.

It should be noted that Neuhoff (**1936**), after examining the type specimen of *Eichleriella incarnata,* concluded that the species should be considered as a later synonym of *Eichleriella spinulosa.*

Specimens examined: Canada: Manitoba, *Buller, Bisby et al,* 24 Sept., 1932; Ontario, *G. D. Darker,* 4 May, 1936, TRT 21378 (NY), 21554 (NY). United States: Idaho, Priest River, *J. R. Weir,* Sept., 1912. Sweden: near Uppsala, *S. Lundell,* 17 Aug., 1927, *S. Lundell,* 29 Nov.,

1927 (NY). Germany: *O. Jaap,* 1904 (Ex. Herb. J. Bresadola, NY). Austria: *L. & C. Rechinger,* Kryptogamae Exsiccatae 1807 (NY). Italy: *J. Bresadola,* 6 Aug., 1898 (NY). France: *Galzin 14674.* United Kingdom (?): Herb. G. Massee (NY).

14. *Sebacina spongiosa* Lloyd, Mycol. Writ. **5**. Mycol. Notes **54**: 779. 1918.

McGuire (**1941**) suggested that this species might be identical with *Sebacina helvelloides* (Schw.) Burt; however, after examining the holotype, I feel that it should be referred to *Sebacina incrustans* (Fries) Tul. Although the purplish-brown exterior is more characteristic of *S. helvelloides,* the interior structure is strongly suggestive of *S. incrustans.* In section there is present a very thick basal layer of relatively thick-walled hyphae, 3–4.5 μ in diameter, which is arranged in distinct ascending strands. The basal layer terminated in a hymenium of basidia which are apparently formed at varying levels. A palisade-like layer of dikaryophyses is not evident; however, the condition of the specimen is such that the exact hymenial organization is not clear. Clamp-connections are absent throughout the basidiocarp. The basidia, 15–18.5 × 10.5–12 μ, and basidiospores, 10–11 × 7.5 μ, are typical of both *S. helvelloides* and *S. incrustans.* In spite of the poor condition of the hymenium, it is possible to state that the species is definitely not a member of the genus *Exidiopsis* and that it probably should be considered as a later synonym of *Sebacina incrustans.*

Specimen examined: Bahama Islands: Nassau, *L. J. K. Brace* (C. G. Lloyd 41458, HOLOTYPE, in BPI).

15. *Sebacina strigosa* Bourd. & Galz., Bull. Soc. Mycol. Fr. **25**: 25. 1909.

A single collection of this species, labeled "*f. typica*" by Bourdot, was examined. In section, the basal regions consist of interwoven hyphae surrounding ascending strands of closely-packed hyphae, the latter forming sterile macroscopically visible projections. The subhymenial hyphae have abundant clamp-connections, and there are clamp-connections at the base of the basidia. The basidia are subglobose to obovate, rarely pyriform, become cruciate-septate, and measure 18.5–22.5(–24) × 12–16.5 μ. The few basidiospores observed were cylindrical to elliptical, ventrally depressed, and measured 12–15 × 7–8 μ.

The dried specimen is a dark reddish-brown crust with adnate margins. The numerous fimbriate, sterile projections are evident at lower magnifications.

The specimen belongs, in my opinion, to the genus *Heterochaete*. It is possibly the same as *Heterochaete macrochaeta* Bres. & Torr. as described by Bodman (**1952**). Since there are several differences between my observations and the original description, and since specimens of the latter species were not examined, it is not possible to state with any degree of certainty that the two names apply to the same species.

Specimen examined: France: *Galzin 3906* (H. Bourdot 6009, PC).

16. *Sebacina subhyalina* Pearson, Brit. Mycol. Soc. Trans. **13**: 71. 1928.

A specimen which Pearson designated as the "type specimen" was examined. The macroscopic and microscopic characters are quite similar to the thin, grayish-hyaline form of *Sebacina podlachica* Bres. It should be considered as a later synonym of Bresadola's name. The basidia are sphaeropedunculate and become separated into a sterile stalk and fertile apical portion. The basidiospores are cylindrical-curved and measure 7–10 × 4–5 μ.

Illustration: Brit. Mycol. Soc. Trans. **13**: 70, *f. 3*.

Specimen examined: England: Sussex, *A. A. Pearson*, 30 Oct., 1926 (PARATYPE, in K).

17. *Sebacina sublilacina* Martin, Mycologia **26**: 262. 1934.
Exidiopsis sublilacina (Martin) Ervin, Mycologia **49**: 123. 1957.

By staining sections of the holotype for 24 hours in equal amounts of 3% KOH, 1% Phloxine, and ammonified 2% Congo Red, the presence of a basidial stalk was demonstrated in this species. Since the stalk becomes devoid of contents and often contorted, its presence has been frequently overlooked, except by Martin (**1934a**) and Whelden (**1935**). Careful examination of fresh collections has shown that the sphaeropedunculate basidium is a characteristic feature of this species.

The sphaeropedunculate basidia, the agglutinate nature of the dikaryophyses and hyphae upon drying, and the capacity to form large, white, mineral accumulations indicate a close relationship to *Sebacina podlachica* and *Exidia nucleata*. Some specimens were examined which had a pustular appearance in section, indicating a relationship with *Stypella minor* and related species.

Additional specimens examined: Massachusetts: *DPR 579*; New York: *DPR 576;* Ohio: *DPR 577;* Iowa: *GWM 1330* (HOLOTYPE), *DPR 2315, 2318, 2319, 2324* and numerous other collections; Oregon: *AM & DPR*, 22 Nov., 1936; California: *KW 383*.

18. *Sebacina uvida* (Fries) Bres. apud Allescher & Schnabl, Fung. Bav. 127. 1891.

Corticium uvidum Fries, Epicr. Syst. Mycol. 565. 1838.

As stated in the discussion of *E. grisea,* the basionym is, according to Lundell (in Lundell & Nannfeldt, **1947**), a synonym of *Corticium lividum* (Pers. ex Fries) Fries; therefore, the name can not be applied to a species of this genus.

SUMMARY

The genus *Exidiopsis* is characterized by resupinate basidiocarps with effused to abrupt margins. The basidiocarps are indeterminate, both in thickness and in width. The tremellaceous basidia are subglobose, ovate, obovate, clavate, or rarely pyriform with an enucleate stalk and arise from lateral proliferations through or near sub-basidial clamp-connections. The basidiospores are varied within the genus but are generally characteristic within the species. They are capable of germinating by repetition. Dikaryophyses may be present or absent. If present, they may consist of slender branching structures only, or as in some species, cylindrical structures may also be present. Clamp-connections are found throughout the dikaryotic hyphae.

Within the genus *Exidiopsis* four subgeneric groupings are apparent, none, however, are sufficiently distinct to warrant a taxonomic designation.

Fifteen species are assigned to the genus, eight are treated as dubious, and eighteen species, which have been assigned to the genera *Sebacina* or *Eichleriella* by other authors, are excluded. Seven new combinations are proposed. A key is presented for the identification of the accepted species.

The numbers of available collections of most species are insufficient for an accurate determination of the geographic ranges. The collections of *Exidiopsis calospora, E. prolifera, E. glaira, E. molybdea, E. fugacissima,* and *E. calcea* examined are mainly from temperate regions. Those of *E. candida, E. mucedinea, E. sublivida,* and *E. alliciens* examined are mainly from subtropical and tropical regions. *E. grisea* seems to be cosmopolitan, whereas the collections made to date of *E. fuliginea, E. laccata, E. macrospora,* and *E. leucophaea* are from limited regions of the world.

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CERCOSPORA SPECIES ON CUCURBITACEOUS HOSTS IN SOUTH INDIA. I. IDENTIFICATION OF SPECIES

G. RANGASWAMI AND S. CHANDRASEKARAN

(WITH 3 FIGURES)

Several cucurbitaceous plants are cultivated in South India as vegetables. Of late *Cercospora* leafspots of some of these hosts have been found to occur in severe forms, sometimes causing leaf blights. Investigations were undertaken to study the diseases in detail, and several cucurbitaceous plants were examined. Recently we (**1960**) reported a new species of *Cercospora, C. annamalaiensis* Rang. & Chandr. on *Luffa acutangula* Roxb. In this paper the systematic position of the fungi on seven hosts is reported.

1. CERCOSPORA CITRULLINA Cke., Chupp, **1953**, p. 185
   Syn.: *Cercospora momordicae* McRae

On living leaves on *Momordica charantia* L., Annamalainagar, Chidambaram and Vallambadugai, Madras, India, February, 1958, S. Chandrasekaran.

Fruiting is amphigenous, stroma is present in the form of globular cells; hyphae are intercellular and intracellular; the conidiophores arise in fascicles through the epidermis and stoma; they are medium brown in color, uniform in width, slightly tortuous with 1 to 3 septa, with visible spore scars and slight attenuation near the apex, ending in subtruncate tips; they measure 3.6 to 5.8 μ in width and 20.3 to 133.4 μ in length. Conidia are hyaline, acicular, multiseptate with 4 to 16 septa, straight to slightly curved, with truncate bases and acute or subacute tips; they measure 3.6 to 6.2 μ in width at thickest point and 23.2 to 139.2 μ in length.

The occurrence of *C. citrullina* on this host in India has been reported by Sydow and McRae (**1929**).

2. CERCOSPORA CITRULLINA Cke. var. **trichosanthei-anguinae** Rang. & Chandr., var. nov.

Maculae obscure albae circulares vel irregulares, diametro 1–5 mm; sub infectione severa nonnullae maculae coalescentes. Fructificationes amphigenae sed potius

hypophyllae; stroma constans e cellulis globosis brunneis et nonnullis mycelii hyphis infra epidermidem. Conidiophori aggregati, per stroma emergentes, plurimum 6–10 in fasciculo quoque, pallide brunnei, uniformes latitudine vel paulum attenuati ad apicem inferiorem, apice superiore rotundato, recti vel tenuiter curvati, septati semel vel bis, sporarum cicatricibus distinctis, 4.4–5.0 μ latitudine ad partem crassissimam, 43.5–188.5 μ longitudine. Conidia acicularia hyalina multiseptata 5–10 septis, recta vel tenuiter curvata, ad basim truncata, ad apicem subacuta, 3.6–4.4 μ latitudine ad partem crassissimam, 20.3–107.3 μ longitudine (Fig. 1).

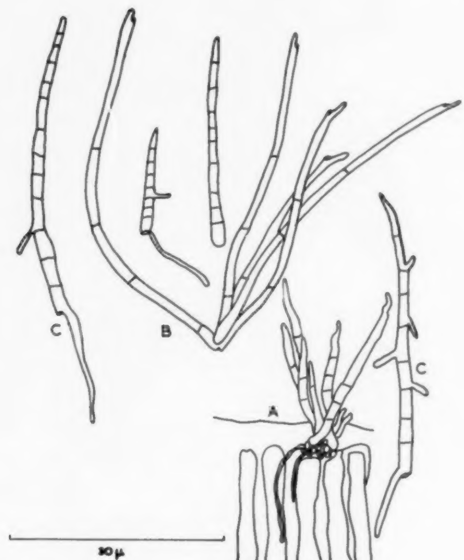

FIG. 1. *Cercospora citrullina* var. *trichosanthei-anguinae* on *Trichosanthes anguina*. A. Transverse section of the leafspot; B. Cluster of conidiophores; C. Conidia, three germinating.

Typus lectus in foliis vivis *Trichosanthei anguinae* L. ad Annamalainagar, in Statu Madras, mense julio 1958 a S. Chandrasekaran, et positus in Herb. Dept. Agri., Annamalai University, Annamalainagar ad in Herb. Crypt. Ind. Orient (HCIO), New Delhi, sub numero accessionis 26667.

Spots dull white, circular to irregular in shape, 1–5 mm; in severe infections two or more spots coalesce. Fruiting amphigenous but chiefly hypophyllus; stroma with brown colored globular cells with a few mycelial strands below the epidermis. Conidiophores in clusters protruding through stomata, 6–10 more common in each cluster, pale brown in color, uniform in width or slightly attenuated towards the distal end,

with rounded tip, straight to slightly curved, with one to two septa, with visible spore scars, 4.4–5.0 μ in breadth at the thickest point and 20.3–107.3 μ in length (FIG. 1).

On the living leaves of *Trichosanthes anguina* L., Annamalainagar, Madras State, India, July 1958, S. Chandrasekaran. Type specimen deposited in the Herbarium of the Department of Agriculture, Annamalai University, Annamalainagar and in Herb. Crypt. Ind. Orient (HCIO), New Delhi (Accession No. 26667).

3. CERCOSPORA CITRULLINA Cke., Chupp, **1953**, p. 185

On living leaves of *Benincasa hispida* Cogn., Chidambaram, Koilampatti and Annamalainagar, Madras, India, January 1959, S. Chandrasekaran.

The fungus is identical with that occurring on *Momordica charantia*. No natural occurrence of *Cercospora* seems to have been reported so far on this host, and this is therefore a new record.

4. CERCOSPORA CITRULLINA Cke., Chupp, **1953**, p. 185

On living leaves of *Cucurbita maxima* Duchesne, Annamalainagar, January 1958, S. Chandrasekaran.

The fungus is identical with those occurring on *Benincasa hispida* and *Momordica charantia*. This seems to be the first record of the occurrence of *C. citrullina* on *Cucurbita maxima*.

5. **Cercospora madrasensis** Rang. & Chandr., sp. nov.

Maculae circulares vel irregulares, diametro 1–8 mm, margine purpureofusco, corona lutea, nonnumquam coalescentes atque formantes maculas multo latiores. Fructificationes amphigenae; stroma constans in cellulis globosis infra epidermidem; hyphae intracellulares et intercellulares. Conidiophori fuscobrunnei, pallidiores ad apices, septis et parietibus fuscobrunneis, uniformes latitudine, recti vel tenuiter curvati, apicibus plurimum truncatis, sporarum cicatricibus distinctis, septis 3–9, cellularum parietibus et septis distincte fuscobrunneis, 2.9–4.4 μ latitudine, 37.7–275.5 μ longitudine. Conidia hyalina, in figuris duabus; nonnulla aciculare gradatim attenuata, alia vero obclavata et ad basim breviter obconica, omnia vero multiseptata septis 4–14, 2.9–3.4 μ latitudine ad partem crassissimam, 26.1–145.0 μ longitudine (Fig. 2).

Typus lectus in foliis vivis *Lagenariae vulgaris* Ser. ad Annamalainagar, in Statu Madras, mense decembri 1958 a S. Chandrasekaran et positus in Herb. Dept. Agri., Annamalai University, Annamalainagar, ad in Herb. Crypt. Ind. Orient (HCIO), New Delhi, sub numero accessionis 26664.

Spots circular to irregular in shape, 1–8 mm in size, purplish dark margin with yellow halos, sometimes coalescing to form large patches.

Fruiting amphigenous, stroma consisting of globular cells beneath the epidermis; hyphae intracellular and intercellular. Conidiophores deep brown, paler towards the tip, septa and walls of the conidiophore dark brown, uniform in width, straight or slightly curved with mostly truncate tip, prominent spore scars, septate with 3–9 septa, cell walls and the septa distinctly dark brown, 2.9–4.4 μ in width and 37.7–275.5 μ in length. Conidia hyaline with two distinct shapes, one acicular with gradual attenuation, the second obclavate with short obconic base, both multiseptate with 4–14 septa, measure 2.9–3.4 μ in width at the thickest point and 26.1–145.0 μ in length (FIG. 2).

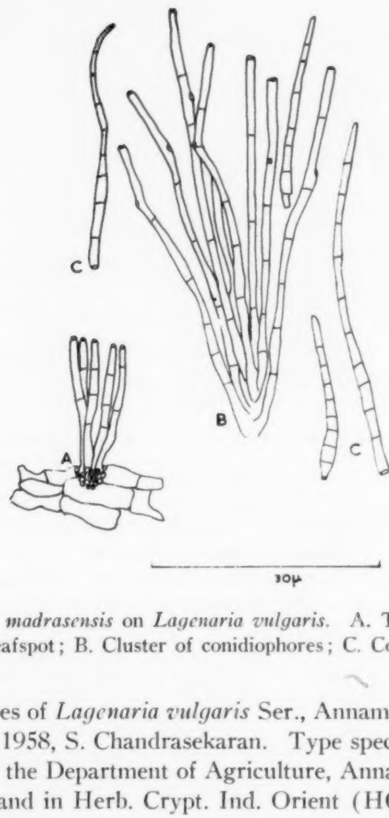

FIG. 2. *Cercospora madrasensis* on *Lagenaria vulgaris*. A. Transverse section of the leafspot; B. Cluster of conidiophores; C. Conidia.

On living leaves of *Lagenaria vulgaris* Ser., Annamalainagar, Madras State, December, 1958, S. Chandrasekaran. Type specimen deposited in the Herbarium of the Department of Agriculture, Annamalai University, Annamalainagar and in Herb. Crypt. Ind. Orient (HCIO), New Delhi (Accession No. 26664).

Salam and Rao (1957) reported *C. lagenariae* Salam & Rao on *Lagenaria vulgaris* Ser. in Andhra Pradesh, central India. This fungus

is characterized by nonseptate conidiophores and cylindric conidia. *C. madrasensis* is distinct from *C. lagenariae* in possessing septate conidiophores and acicular to obclavate, never cylindric, conidia and also in the conidiophore and conidial measurements.

6. **Cercospora chidambarensis** Rang. & Chandr., sp. nov.

Maculae pallide virides ab initio, postea luteae, demum obscure albae, marginibus angustis olivaceo-brunneis in superficie superiore, marginibus indistinctis in superficie inferiore, circulares vel irregulares ambitu, 0.5–6 mm magnitudine, nonnumquam coalescentes atque operientes totum folium. Fructificationes amphi-

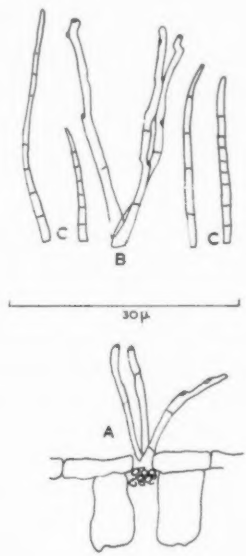

FIG. 3. *Cercospora chidambarensis* on *Cucumis sativus*. A. Transverse section of the leafspot; B. Cluster of conidiophores; C. Conidia.

genae; stroma constans e cellulis globosis infra epidermidem; conidiophori laxe fasciculati, colore brunneoli, uniformes latitudine, sparse septati, septis singulis ternisve, tenuiter flexuosi, truncati vel subtruncati ad apicem atque ornati cicatricibus distinctis sporarum, 3.6–5.1 µ latitudine, 20.3–159.2 µ longitudine. Conidia hyalina, acicularia, recta vel tenuiter curvata, multiseptatis, septis 4–8, truncata ad basim, subacuta ad apicem, 2.9–4.4 µ latitudine ad partem latissimam, 17.4–149.0 µ longitudine.

Typus lectus in foliis vivis *Cucumis sativis* L. ad Chidambaram in Statu Madras, mense januario 1958 a S. Chandrasekaran et positus in Herb. Dept. Agri., Anna-

malai University, Annamalainagar ad Herb. Crypt. Ind. Orient (HCIO), New Delhi, sub numero accessionis 26666.

Spots pale green in the early stages, later turning yellow and then dull white, with narrow olive brown margin on the upper surface and indistinct margin on the lower surface, circular to irregular in shape, 0.5–6.0 mm, sometimes coalescing and covering entire leaf. Fruiting amphigenous; stroma consisting of globular cells below the epidermis; conidiophores in loose fascicles, medium brown in color, uniform in width, sparsely septate with 1–3 septa, slightly tortuous, truncate to subtruncate tip and with visible spore scars, 3.6–5.1 μ in width and 20.3–159.2 μ in length. Conidia hyaline, acicular, straight to slightly curved, multiseptate with 4–8 septa, truncate base and subacute tip, 2.9–4.4 μ in width at the thickest point and 17.4–149.9 μ in length (FIG. 3).

On living leaves of *Cucumis sativus* L., Chidambaram, Madras State, January, 1958, S. Chandrasekaran. Type specimen deposited in the Herbarium of the Department of Agriculture, Annamalai University, Annamalainagar and in Herb. Crypt. Ind. Orient (HCIO), New Delhi (Accession No. 26666).

7. CERCOSPORA COCCINIAE Munjal, Lall & Chona

On living leaves of *Coccinia indica* Wt. & Arn., Annamalainagar, February, 1958, S. Chandrasekaran.

An unidentified species of *Cercospora* was described by Jain (**1950**) from North India. Munjal et al. (**1959**) described a new species for the fungus which was collected from Punjab in 1954. Chupp (1959), in a private communication to us, was of the opinion that this fungus might be similar to *C. echinocystis* Ell. & Mart. and *C. elaterii* Passerini. But careful examinations made by us revealed that the fungus on *Coccinia indica* differed from the above two species. In the meantime Munjal et al. (**1959**) described a new species for the fungus. The descriptions given for *Cercospora cocciniae* are identical with those of the fungus collected by us.

Of the four species of *Cercospora*, three and a variety of one were cultured and their physiological properties and pathogenicity tested. Further distinguishing characters for the species are being reported elsewhere.

The authors are thankful to Rev. H. Santapau for the Latin diagnosis of the new species reported here.

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SOME VIEWPOINTS ON THE PHYLOGENY OF RUST FUNGI. IV. STEM RUST GENEALOGY [1]

E. E. LEPPIK

(WITH 5 FIGURES)

Since the discovery and first description of the black stem rust, *Puccinia graminis*, by Persoon (**1794, 1801**), more attention has been devoted to this species than to any other rust on cultivated plants. This is due partly to the great losses caused by stem rust in all grain-growing countries, and partly to the persistent interest of uredinologists in the life history of the heteroecious rusts. Recent investigations of heterothallism, physiologic races and hybridization among stem rust strains have contributed much to our knowledge about the genetic constitution and mechanism of inheritance of rust fungi. This in turn has rendered valuable service to plant breeders in their search for rust-resistant crop varieties.

Eriksson (**1894**) and Stakman and Piemeisel (**1917a, b**) showed that the enormous population of *Puccinia graminis* is not a uniform taxon, but is composed of numerous varieties, physiologic races and biotypes that differ from one another in pathogenicity and infection types produced on various host plants. These subspecific units are in a constant flow of changes and adaptations in response to the evolving host plants and ever changing genetic environments in cultivated plants. Through the modification of cereal crops, man is stimulating the development of new rust races. Johnson (**1961**) recently called this a "man-guided evolution in plant rusts."

In spite of the great economic importance of the stem rust and increasing scientific interest devoted to its biology and pathogenicity, only little is known about the phylogeny and evolution of the *Puccinia graminis* complex. In most outstanding monographs and manuals, referred to at the end of this paper, little information is given about the origin and

[1] Reports I, II and III of this series were published in Mycologia **45**: 46–74, 1953; **48**: 637–654, 1956; and **51**: 512–528, 1959.

Journal Paper No. J-4215 of the Iowa Agricultural and Home Economics Experiment Station, Ames, Iowa. Project No. 1490.

genetic relationships of stem rust varieties and races that prefer to attack culms and hard sheaths of grain crops and grasses.

There are extensive taxonomic treatises of rust fungi published by the Sydows (**1904**), Fischer (**1904**), Arthur (**1907–1912, 1934**), Grove (**1913**), McAlpine (**1906**), Liro (**1908**), Klebahn (**1914**), Dietel (**1928**), Guyot (**1938**), Joerstad (**1940**), Săvulescu (**1941, 1953**), Cummins (**1956**), Gäumann (**1959**), and others. But almost everyone of these authors employed his own method of classification, arranging rusts species according to telial hosts (Sydow), life cycles (Arthur), morphology of teliospores (Klebahn), or telial morphology (Gäumann). All these artificial systems are selected for their convenience in practical identification of rusts and serve well their special purpose in the absence of natural phylogenetic systems. It is but natural, therefore, that stem rust should hold a place in these systems apart from its phylogenetic relatives.

In this paper, therefore, an attempt is made to sketch briefly the life history of stem rust and its verifiable relatives on the basis of phylogenetic evidence and the present biological specialization of these rusts on their hosts. This method of study provides a new approach to the problem of origin and evolution of rust fungi from the hologenetic viewpoint, as described and discussed elsewhere (Leppik, **1953**, **1955**, **1956**, **1959**). In this brief review, however, no effort is made at complete coverage of enormous literature of the subject, except quoting some monographic treatises by the Sydows (**1904**), Lehmann et al. (**1937**), Cummins (**1956**), and Gäumann (**1959**). Nor can the problem of physiologic and pathogenic races of stem rust be discussed at length and the reader is referred to the review articles by Levine (**1923**), Levine and Cotter (**1932**), Stakman et al. (**1930, 1934**), Reed (**1935, 1946**), Johnson (**1949, 1954**), Stakman (**1954, 1957**), Carson (**1957**) and Stewart et al. (**1959**). Not less important economic aspects and the complexity of breeding work to obtain rust-resistant cultivars are reviewed by Newton et al. (**1930**), A. M. Brown (**1940**), Stakman (**1954, 1957**), Mehta (**1940**), Hingorani (**1952**), Hart (**1955**), and many others.

VERIFIABLE RELATIVES OF STEM RUST

Forming its telial stage mainly in culms and hardened leaf sheaths, stem rust occupies a rather unique place in the midst of numerous grass rusts which inhabit soft-tissued leaves only. Uredia are less consistent in their habitation and may develop on culms, leaves, and bracts, occasionally mixing or being mixed with the sori of other rust species.

Such topological [2] specialization makes it difficult to find from the mass of leaf rusts those species which might be genetically related with stem rust. Some authors (Gäumann, **1959**) consider stem rust itself to be a collective taxon, composed of many species which other workers interpret as varieties.

Looking for stem rust relatives, one can first examine *Puccinia culmicola* Diet. (Asuyama, **1935**), *P. sesleriae-coeruleae* [3] Fischer, *P. anthoxanthi* Fuckel, and *P. avenae-pubescentis* Bubák. All these species show a striking similarity to stem rust in their main morphological characteristics and are able to infect *Berberis* in cultures. In nature these rusts, ignoring barberry, pass the winter in uredial stage inside of their gramineous hosts. A close relationship of these species with stem rust is generally accepted by recent uredinologists (Arthur, **1934**; Gäumann, **1959**).

Puccinia phlei-pratensis [3] Erikss. & Henn. differs from stem rust by somewhat smaller spores in all stages and by a more slender mycelium. Many authors treat this rust as a highly specialized variety of *P. graminis* (Arthur, **1934**, p. 176); others (Gäumann, **1959**, p. 767) consider it to be an independent species. It occurs on stems, leaves and sheaths of *Phleum pratense* L., *P. arenarium* L. and *P. michelii* All. Using a North American race, Johnson (**1911**) could infect *Arrhenatherum elatius* (L.) M. & K., *Avena sativa* L., *Dactylis glomerata* L., *Festuca pratensis* Huds. (= *F. elatior* L.), *Poa compressa* L., and *Secale cereale*

[2] In this paper topological specialization (topos = place) means the dependence of pathogens on certain plant organs, such as roots, stems, leaves, fruits, or seeds. Also included in this group are epiphyllous, hypophyllous and amphigenous (growing on upper, lower or either side of a leaf) rusts. This new term is analogous with biological and physiological specialization of rusts on certain host groups.

[3] In accord with the International Code of Botanical Nomenclature Art. 24 (Lanjouw, **1956**, p. 24), simple trinomial names, such as *Puccinia phlei-pratensis* Erikss. & Henn., are hyphenated in this paper. In common practice, however, the hyphen is used to indicate special host-rust connections of the heteroecious species with two hosts in a life cycle. *Puccinia caricis-montanae* Ed. Fisch., for instance, has its teliospores on *Carex* and aecia on *Centaurea montana* L. A provisional *Puccinia caricis montanae*, on the contrary, could be a rust on *Carex montana* L., as *Puccinia phlei pratensis* is a rust on *Phleum pratensis*.

This is a convenient method to distinguish biologically specialized rust species that frequently do not possess clear morphological characteristics for their classification. It is actually an extension of an old custom introduced by Klebahn (**1892**), long practiced by classic uredinologists (Fischer, **1904**), and accepted as a rule by Gäumann (**1959**, p. 11) in his recent "Die Rostpilze Mitteleuropas." The question is worthy of consideration in the mycological section of some future International Botanical Congress.

Vill. All are hosts of stem rust. But no teliospores were formed on these secondary hosts of timothy rust in cultures. Evidently this rust cannot survive on the above-mentioned plants and Johnson's experiment points merely to the close genetical relationship between both the timothy and stem rusts. Eriksson and Henning (**1894**) reported infection of *Berberis vulgaris* L., but repeated attempts by many workers have completely failed to infect barberry or any other plant with basidiospores of timothy rust (Gäumann, **1959**, p. 768). These facts indicate that timothy rust abandoned its primary aecial host, has taken its own way of specialization, and is gradually outdistancing its parental stem rust complex. Its great vitality and rapid expansion in the New World provide necessary prerequisites for a possible removal of the aecial stage from the antique *Berberis* to some more modern group of angiosperms. There are many such examples among progressive Melampsoraceae and Pucciniaceae where the rusts have changed their life cycle, transferring one generation from the phylogenetically older host to more modern plants groups (Leppik, **1953**, **1956**, **1959**).

Puccinia dactylidis Gäum. on *Dactylis glomerata* L. in Switzerland is frequently mixed with *P. graminis* and *Uromyces dactylidis* Otth, all of which occur on the same plant. According to Gäumann (**1959**, p. 763, 768) this rust is morphologically similar to *P. graminis,* but its basidiospores do not infect *Berberis, Ranunculus, Ficaria, Rumex,* or any other plant so far tested. Thus considerable morphological and phylogenetic evidence indicates that all above-mentioned rust species are related genetically and could be joined into a group of close relatives of the black stem rust.

In a previous paper (Leppik, **1959**, p. 515) a new term "sept" was used to indicate natural groups of closely related species which descend from a common ancestral stock. The members of a sept must resemble each other in their morphological structure and biological specialization, or show any other evidence about their close phylogenetic relationship.

Most frequently a sept is formed by the splitting of a large and polymorphic species into new races and varieties which gradually acquire more and more morphologic distinctions and are finally recognized as independent species by taxonomists. Beside such microspecies the close relationship of correlated microcyclic forms on related hosts is easily detectable and frequently indicated in recent manuals (Arthur, **1934**; Gäumann, **1959**).

The next higher phylogenetic units that follow "sept" were called "clan" and "kin." If several related septs show sufficient resemblance in their main characteristics, and evidently descend from common an-

cestors, they can be united into a definite "clan." Related "clans" can be further united into a "kin," and so on, until some conventional taxonomic unit, series or subsection, is reached.

It seems practical to derive the names for these lowest generic subdivisions from the most typical representative in the group, or to use some other morphological or biological characteristics in accord with the International Code (Lanjouw, 1956, Art. 22).

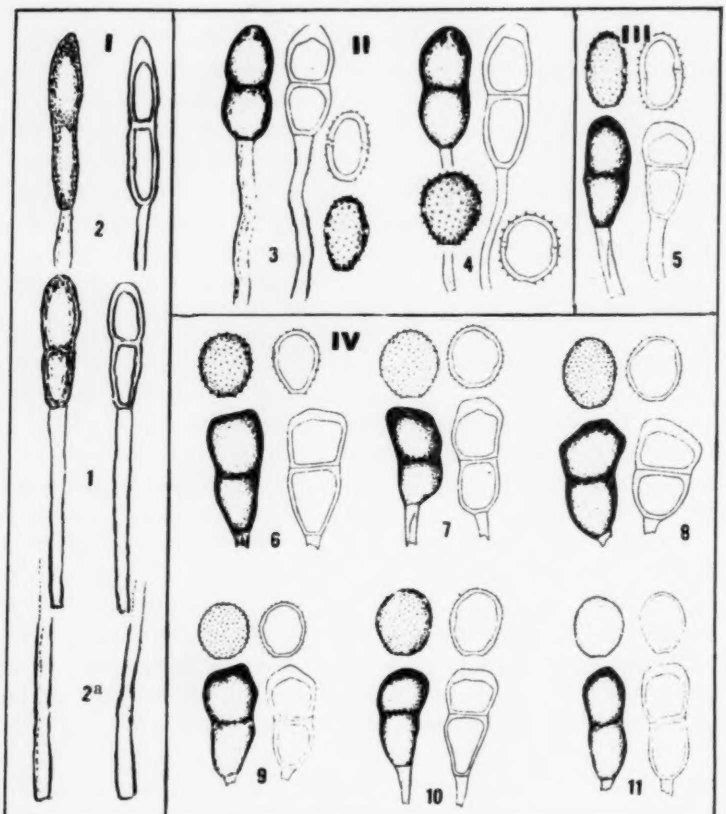

FIG. 1. Stem rust alliance. I. Sept Berberidis: 1. *Puccinia meyeri-alberti.* 2. *P. berberidis* with long pedicels (2a). II. Sept Phragmitis: 3. *P. phragmitis.* 4. *P. arundinariae.* III. Sept Graminis: 5. *P. graminis.* IV. Sept Pygmaea: 6. *P. pygmaea.* 7. *P. glumarum.* 8. *P. montanensis.* 9. *P. hordei.* 10. *P. koeleriae.* 11. *P. poae-sudeticae.* 1, 2 after Sydow, 3–11 after Cummins.

Introduction of these small genealogical units of verified relationship is justified in a huge group such as the *Uromyces-Puccinia* complex. In this mass of species the true genetic relationship between larger taxonomic units such as series and sections probably never can be correctly established. Gäumann (**1959**) recognized the necessity of such phylogenetic units in using terms "Verwandtschaftskreis" and "Formenkreis" in his recent treatise on rusts of Central Europe. For the genealogical study, as proposed in this paper, the grouping of species according to their genetic relationship is almost unavoidable.

The main objection that may be raised against this new method of classification is the obvious difficulty of establishing the exact genetic relationships among the huge number of rust species in the *Uromyces-Puccinia* complex. This difficulty, however, can be partly surmounted now by application of comparative hologenetic methods for the rust study. It is generally accepted that the biological specialization of rust fungi must necessarily have evolved parallel with the evolution of their hosts. Accordingly, the close relatives of stem rust must be restrained within the host sector which has its center and beginning on barberry, and its spread on gramineous plants (FIG. 2).

RELATED RUSTS ON BARBERRY (FIG. 1)

Two large clans, *Longipedicellae* and *Brevipedicellae*, both subdivided into many septs, inhabit with their aecia the genus *Berberis*, and with telia numerous genera of gramineous plants. Both these clans have much homology in their morphological characteristics and occupy a common host sector, so that their descent from a common stock seems a highly persuasive interpretation.

PUCCINIA clan **Longipedicellae** (FIG. 1 : I, II)

Aecidiis pseudoperidiis cupuliformis vel breviter cylindraceis in *Berberidis* vel *Mahonia* viventis. Teliosporae oblongo-clavatae, ad apicem rotundatae; pedicello longo, persistenti. TYPUS: *Puccinia graminis* Pers.

The clan *Longipedicellae* has more primitive teliospores and is probably older phylogenetically than the clan *Brevipedicellae*, resembling with its long and slender pedicels some species of *Cumminsiella*, living also on *Berberis* and *Mahonia*.

Sept **Berberidis** (FIG. 1 : I).

Uredineae microcyclicae in Berberidaceae viventis. Aecidiis cupuliformibus vel breviter cylindraceis, albo-flavidis, in foliis vivis vel fructibus evolutis. Teliis hypophyllis, minutis vel mediocribus, plerumque pulvinatis. Teliosporae oblongo vel

oblongo-clavatae, ad apicem rotundatae; pedicello longo, hyalino vel brunneis, persistenti.

More distantly related to stem rust is obviously the group of autoecious rusts which live on *Berberis* in South America: *Puccinia berberidis* Mont. on *Berberis glauca* Kunth. in Chile; *P. meyeri-alberti* P. Magn. on *B. buxifolia* Lam., *B. congestiflora* Gay, *B. darwinii* Hook., *B. actinocantha* Mart., *B. blaurina* Bellb., *B. chilensis* Gill., *B. ruscifolia* Lam. (Sydow, **1904**; Jackson, **1927**), *B. linearifolia* Phil., and *B. pearcei* Phil. in Chile; *P. berberidis-trifoliae* Diet. & Holw. on *Mahonia swasey* (Buekl.) Fedde (*B. trifolia* Schult.) in Mexico. These species have teliospores with long pedicels and closely resemble stem rust. They are both structurally and physiologically correlated with *P. graminis*. But considering the old age and geographic isolation of these species, they could be separated into a different sept *Berberidis* or united with *Culmicola* in the same clan *Longipedicellae* (see below).

Sept *Berberidis* represents a collection of brachycyclic and microcyclic species, all autoecious forms with telia on *Berberis* or *Mahonia* in South America (Spegazzini, **1921**). Evidence is strong, therefore, that these are relicts from the ancient rusts which lived on *Berberis-Mahonia* complex in the northern hemisphere, during early Tertiary (see below). Driven southward by the Pleistocene glaciers and disconnected from their original telial hosts, by necessity, these rusts reduced their life cycle to the former aecial host only.

There are several examples among puccinioid rusts where the ancient geological forms exist today side by side with more recent types on closely related hosts. Newton and Johnson (**1937**) showed experimentally that if the wheat stem rust races 9 and 36 were crossed, the hybrid may produce uredia and telia on *Berberis* together with usual spermagonia and aecia. Apart from sexual crossing Bridgmon (**1959**) obtained new races of *Puccinia graminis* var. *tritici* by vegetative fusion.

Sept **Phragmitis** (FIG. 1: II).

Aecidiis cupuliformis, albo-flavidis in foliis vivis viventis. Teliosporae oblongo-clavatae, ad apicem rotundatae; pedicello longo, persistenti. TYPUS: *Puccinia phragmitis* (Schum.) Koern.

A group of closely related species, which are structurally correlated with stem rust, lives with their telia on *Phragmites communis* Trin. and with aecia on various higher angiosperms. A close relationship between *P. phragmitis* (Schum.) Koern. (0, I, II, III), *P. ornata* A. & H. (III), *P. traillii Plowr.* (0, I, II, III), *P. trabutii* Roum. & Sacc. (0, I, II, III), *P. obtusata* Otth (I, II, III), and *P. inulae-phragmiticola* Tranzch.

(I, II, III) has long been recognized by Dietel (**1897**, **1918**), Fischer (**1904**), Gäumann (**1959**), and Gäumann and Poelt (**1960**). As a natural group of closely related species with the obvious gene-center on *Phragmites* they can be united into a sept *Phragmitis.*

All these species have ellipsoid teliospores with long pedicels, oblong or ellipsoid urediospores with equatorial pores, and cupulate aecia with globoid, finely verrucose aeciospores. The main difference between the septs *Culmicola* and *Phragmitis* is that the latter has white (actually colorless) aecia and a distinct host range. The host sector of the sept *Phragmitis,* however, is actually a continuation of that of the *Culmicola* (FIG. 3). This condition indicates that the ancestors of sept *Phragmitis* have obviously separated from the Berberidae complex by removing their aecia from *Berberis* to Polygonaceae. The firm teliospores with long hard pedicels of the sept *Phragmitis* appear more primitive in their structure than the more delicate spores of the sept *Culmicola.*

The sept *Phragmitis* forms its telia on *Phragmites communis* only, but has a very large range of aecial hosts among numerous higher families of angiosperms. *P. trabutii* [= *P. isiaceae* (Thuem.) Wint.], for instance, occurs on 77 host species of 52 genera and 19 families of angiosperms (Dietel, **1918**; Guyot and Massenot, **1958**; Gäumann, **1959**).

The sept *Phragmitis* has followed the general rule of the irreversibility of biological specialization of rust fungi, as stated first by this writer (Leppik, **1947**) and described more fully in a successive paper (**1953**, p. 69). According to this rule a heteroecious rust can transfer one phase (i.e., telial or aecidial) at a time from its previous host to new hosts which must be phylogenetically younger than the original host of departure. For instance, it is fairly clear that *Berberis* is a primary host for *Puccinia graminis* from which host the stem rust has distributed to numerous gramineous plants. For *Puccinia phragmitis,* on the contrary, *Phragmites communis* is the primary and *Rheum* and *Rumex* are secondary hosts. Such unilateral radiation of rust species from the original center of distribution to numerous new hosts is demonstrated in FIGS. 2 and 3. The phenomenon itself can be explained by the irreversible evolution of genetic constitution of rusts in response to the ever evolving genetic change in hosts. Thus a usable method is available now to estimate the relative phylogenetic age of present day rust groups and their host taxa.

As a matter of fact, aecia of *P. trabutii* have never been found on phylogenetically older host families, such as Ranunculaceae, Rosaceae, Berberidaceae, Rhamnaceae, and Urticaceae. Guyot and Massenot (**1958**, p. 540) have successfully infected 50 higher plants, such as those

listed above by Gäumann (**1959**, p. 752), but they could not obtain positive reaction on *Berberis vulgaris* L., *Clematis vitalba* L., *Delphinium consolida* L., *Plantago lanceolata* L., *Ranunculus repens* L., *Rhamnus cathartica* L., *Ribes grossularia* L., *Urtica dioica* L., *Urtica urens* L., and on many other phylogenetically older plants.

This fact indicates that the sept *Phragmitis* has possibly shifted its heteroecism a step higher, abandoning its primary aecial hosts on older angiosperms (assumably *Berberis*), and radiated from the present telial host (*Phragmites communis*) to modern flowering plants.

Sept *Phragmitis* is distributed through the northern hemisphere and occurs also in South America (*P. phragmites*) and Africa (*P. trabutii*),

In a previous paper an attempt was made to derive the *Uromyces-Puccinia* complex from the ancient Gymnosporangiaceae which might have resembled the primitive *Gymnotelium* (Leppik, **1959**). If this assumption is correct, the teliospores of more primitive species of the genus *Puccinia* should have a very long pedicel, such as that of the subgenus *Gymnotelium*, and more advanced species, short ones. Such evolutionary sequence from the long and firm pedicels of *Eupuccinia* toward the short or nearly disappearing pedicels of section *Bullaria* is almost unanimously accepted by recent uredinologists (Arthur, **1934**; Cummins, **1936**; Gäumann, **1959**).

According to this view the sept *Phragmitis* could be phylogenetically somewhat older than the sept *Culmicola*, both developed from a common ancestral stock of the clan *Longipedicellae* on *Berberis*. This view is also supported by the fact that the host genus *Phragmites* is geologically a very old and stable taxon with only three recent species.

Puccinia arundinariae Schw. (II, III) on the very old genus *Arundinaria* has similarly long pediceled teliospores and urediospores with equatorial pores. Whether or not this rust is related to the sept *Phragmitis* is difficult to judge, since the aecia (*Aecidium smilacis* Schw.?) and whole life cycle of this rust remain unknown.

Closely related to reed rust seems to be the European sept *Moliniae* on *Molinia* (telia) and on various angiosperms (aecia). *P. moliniae* (Tul.) Rost., *P. brunellarum-moliniae* Cruchet, and *P. nemoralis* Juel, have teliospores with long and hard pedicels, urediospores with equatorial pores, and white aecia, much like those of the sept *Phragmitis*. This sept may also be derived from the clan *Longipedicellae* on *Berberis*.

Sept **Culmicola**, culm rusts (FIG. 1: III).

Spermogoniis et aecidiis in foliis vivis *Berberidis* vel fructibus *Mahoniae*, urediis et teliis in Gramineae viventis. Aecidiis pseudoperidiis cupuliformibus vel breviter cylindraceis, flavidis. Urediosporis ellipsoideis vel ovato-oblongis, echinulatis, poris

germinationis saepe quattuor, aequatorialibus instructis. Teliis plerumque in culmis et vaginis, saepe etiam in foliis evolutis, mox nudis, pulvinatis, atris. Teliosporae oblongo-clavatae, ad apicem rotundatae; pedicello longo, persistenti. TYPUS: *Puccinia graminis* Pers.

Puccinia graminis Pers. (0, I, II, III), *P. culmicola* Diet. (0, I, II, III), *P. anthoxanthi* Fuckel (0, I, II, III), (= *P. graminis*, subsp. *minor* Guyot & Massenot, **1958**), *P. avenae-pubescentis* Bubak (0, I, II, III), *P. dactylis* Gäum. (II, III), and *P. phlei-pratensis* Erikss. & Henn. (II, III), can be united into the sept *Culmicola,* or culm rusts. This sept is distinguishable by its occurrence mainly on culms and the sheath (telia) or leaves (uredia) of Festucoideae and by the formation of aecia (if any) on *Berberis* or *Mahonia.* Further characteristics of this sept are yellow, cupulate or cylindric aecia, and oblong or ellipsoid urediospores with four equatorial pores. Telia are naked, teliospores with long and firm pedicels. Sept *Culmicola* has a cosmopolitan distribution.

Further members of this sept could be found among imperfectly known grass rusts, such as *P. heimerliana* Bubák (II, III), *P. trebouxii* Sydow (II, III), *P. imperatae* (Magn.) Poir. (II, III) and others.

Occasionally long cylindrical aecia are found on *Berberis* leaves, whose life cycle and taxonomic position are still unknown. The writer collected such cylindric aecia on *Berberis vulgaris* on the Swiss Alps (Zermatt) in 1928, and indicated the rust as a possible new variety of *P. graminis* (Leppik, **1956**, p. 641, footnote).

PUCCINIA clan **Brevipedicellae**

Aecidiis pseudoperidiis cupuliformis (Fig. 1: IV). Teliosporae ellipsoidis, obtusis vel truncatis, basi rotundatis; pedicello brevissimo, saepe subnullo. TYPUS: *Puccinia brachypodii* Otth.

Parallel with the stem rust relatives, another clan *Brevipedicellae* forms its aecia on *Berberis* and its telia on various gramineous plants. This clan is characterized by its clavate, short pedicelled teliospores and broadly ellipsoid or globoid urediospores with scattered pores. It has its beginning on *Berberis,* but numerous more advanced septs are alternating between grasses and higher angiosperms. Both clans, *Longipedicellae* and *Brevipedicellae,* must necessarily be distantly related and could be united into a joint kin, *Berberidae.*

A few septs of the large clan *Brevipedicellae* which have some interest from the standpoint of stem rust genealogy are listed below.

Sept **Pygmaea** (FIG. 1: IV).

Aecidiis pseudoperidiis cupuliformis. Soris teliosporiferis hypophyllis, minutissimis, semper epidermide tectis; pedicello brevissimo, saepe hyalino. TYPUS: *Puccinia pygmaea* Erikss.

Eriksson (**1895**) has chosen the epithet "pygmaea" for a grass rust which is characterized by very small hypophyllous telia, covered for a long time by epidermis. In early growth the tiny telia of this rust are scattered over the leaf surface, and are scarcely noticeable. Later on, however, they become arranged into long dark lines which are easily detectable by a magnifying glass.

The name *"Pygmaea,"* therefore, can be applied to the whole sept of related species with pygmaean telia on grasses and tiny aecia on *Berberis* or *Mahonia*. Further characteristics of this sept are: globoid or ellipsoid urediospores with scattered pores, and clavate, short-pedicelled teliospores, frequently mixed with dark-brown subepidermal paraphyses. Compact telia remain long covered by epidermis and are clearly distinguishable from the naked telia of stem rust relatives.

Ordinary members of the sept *Pygmaea* are *Puccinia pygmaea* Erikss. (0, I, II, III), *P. arrhenatheri* (Kleb.) Erikss. (0, I, II, III), *P. brachypodii* Otth (= *P. baryi* (Berk. & Br.) Winter) (0, I, II, III), *P. montanensis* Ellis (0, I, II, III), *P. glumarum* (Schm.) Erikss. & Henn. (II, III) (?), *P. koeleria* Arth. (0, I, II, III), *P. milii* Erikss. (II, III) (?), and *P. poae-sudeticae sensu* Joerstad (0, I, II, III) (?). Some other species among grass rusts whose life cycles are not yet wholly known very likely belong to this sept.

Known host range of the sept *Pygmaea*, not including the hosts of *P. glumarum*, for the aecial and telial stage are: *Berberis* spp. and *Mahonia aquifolium* Nutt.; tribe *Avenae: Agropyron* spp., *Arrhenatherum* spp., *Brachypodium* spp., *Calamagrostis* spp., *Elymus* spp., *Hordeum jubatum* L., *Koeleria cristata* (L.) Pers., *Melica imperfecta* Trin., *Milium effusum* L., *Sitanion hystrix* (Nutt.) J. G. Sm. Sept *Pygmaea* is distributed on the northern hemisphere.

Sept **Rubigo-vera.**

Aecidiis cupuliformis. Soris teliosporiferis epidermide tectis, atris; pedicello brevi. TYPUS: *Puccinia rubigo-vera* (DC.) Wint.

This sept is distinguishable from the pygmaean rusts for its aecial hosts only, which are formed on Boraginaceae. Members of this sept are so similar to each other morphologically that Arthur (**1934**) united all of them under the name *P. rubigo-vera* (DC.) Wint. into a single species. Cummins and Caldwell (**1956**) renamed this collective species *P. recondita* Rob. Gäumann (**1959**), however, preferred to keep these

small forms as independent species, but joined them into a "Formenkreis" of *P. rubigo-vera* (DC.) Wint., thus indicating their close relationship with each other.

For the genealogic study in this paper, we adopt Gäumann's classification which reflects better the interrelationship of the species involved.

Following species can be included in the sept *Rubigo-vera:*

P. aegilops Maire (0, I), on *Anchusa* spp., *Borago officinalis* L., *Cynoglossum* spp., *Lithospermum arvense* L., *Solenanthus lanatus* DC. (II, III), on *Aegilops* spp.; *P. cerinthes-agropyrina* Tranzs. (I), on *Cerinthe minor* L., *Cynoglossum creticum* Mill., *Echium* spp., *Lithospermum* spp., *Myosotis* spp., *Omphalodes linifolia* Moench; *P. symphyti-bromorum* F. Müller (0, I), on *Anchusa* spp., *Borago* spp., *Nonnea* spp., *Pulmonaria* spp., and *Symphytum* spp. (II, III), on *Bromus* spp.; *P. dispersa* Erikss. (0, I), on *Anchusa* spp. (II, III), on *Secale* spp.; *P. arnaudi* Hariat & Diet., microcyclic (III), on *Echium vulgare* L., *Lithospermum* spp., and *Pulmonaria* spp.

Sept *Rubigo-vera* is distributed throughout the northern hemisphere with exception of *P. arnaudi* which is restricted to south Europe. Further related septs of the clan *Brevipedicellae* will be described elsewhere.

DIFFERENTIATION OF STEM RUST RELATIVES ON GRASSES

The above described phylogenetic classification of septs, clans, and kins may give us a preliminary picture of the evolution of stem rust and its relatives on angiosperms. Undoubtedly there lived an ancestral stock of heteroecious puccinioid rusts on antique barberry which had their alternate telial stage on ancient gramineous plants. Very likely these rusts were characterized by cupulate aecia, ovate or globoid urediospores, and ovate two-celled teliospores with a long firm pedicel in open telia.

Differentiation in this ancient rust stock must have taken place with the progression of the gramineous plants and expansion of the grassland areas in the northern hemisphere.

There must have been an early trend toward the shortening of the pedicels of teliospores. This trend evolved parallel with the tendency of telia to remain covered for a long time by the epidermis of the host plant, being in this way better protected during their resting stage in winter. It appears that the rusts of the covered telial type are best fitted to live on Cyperaceae and Gramineae in the northern hemisphere. The covered telial type prevails over the telia in the ratio of 4 to 1, if the number of rust species on the present-day sedges and grasses is consid-

ered. This evolutionary trend of grass rusts is in agreement with Gäumann's view (**1959**, p. 427) that the teliospores with firm persistent pedicels are older geologically.

Prevalent rusts on Compositae, Umbelliferae and other higher angiosperms belong to the *Bullaria*-type which is characterized by open aecia, globoid or ellipsoid teliospores with very short and fragile pedicels. Such powdery teliospores are less adequately protected than are the covered types, but they take part in distribution. The subgenus *Bullaria* is generally recognized as the geologically youngest group of the genus *Puccinia* (Arthur, **1934**; Gäumann, **1959**).

Thus a well traceable trend is represented in the evolution of teliospores of the genus *Puccinia*. Geologically oldest forms are oblong, rounded at each end, and with long persistent pedicels, similar to the teliospores of the genus *Gymnotelium*. In this stage they are formed in open telia. In the next stage the pedicels are much reduced, but still firm and persistent, developing long-covered telia. The youngest stage is characterized by powdery teliospores with short and fragile pedicels in open telia.

HOST RANGE AND BIOLOGICAL SPECIALIZATION OF STEM RUST

As a macrocyclic heteroecious rust, *Puccinia graminis* requires two alternate hosts to complete its full life cycle. The aecial stage regularly occurs on *Berberis* and infrequently on *Mahonia*, whereas the telial stage can live on gramineous plants only. Basidiospores, which develop from the overwintered telia on grasses, are able to infect the leaves of *Berberis* and berries of *Mahonia*. Aeciospores, on the contrary, cannot reinfect barberry but have to continue their life on some cereals or grasses. However, this rhythmic alternation of generations is disproportionately divided among its hosts. To the extremely limited number of genera of aecial hosts in Berberidaceae corresponds not less than 80 genera with several hundred species of telial hosts in the grass family (FIG. 2). From any one of these telial hosts stem rust sooner or later has to return to *Berberis* for the sexual revitalization of its germ plasm.

From the recent phylogenetic study (Leppik, **1959**) it appears that historically barberry is the primary host and grasses secondary hosts for stem rust. This means that the differentiation of this rust species must have occurred on an ancient barberry and some unknown telial host, from which the fungus has spread to numerous gramineous plants, as pictured in FIG. 2. Consequently we can analyze the biological specialization of stem rust according to this host sequence, beginning with its aecial stage on barberry.

That stem rust is specialized to live on *Berberis* and *Mahonia* indicates the close biochemical relationship between both these host genera. But there is also considerable morphological and cytological evidence in favor of some authors who join both genera into a single subtribe Berberidinae (Janchen, **1949**, p. 23; Tischler, **1902**). Dermen (**1931**) went a step further and suggested joining both *Berberis* and *Mahonia* into a single genus. On the basis of his chromosome study he concluded that cytogenetic data do not justify the separation of these two taxa into different genera.

The close genetic relationship between these two taxa is further evidenced by several intergeneric forms, called *Mahoberberis*, which are

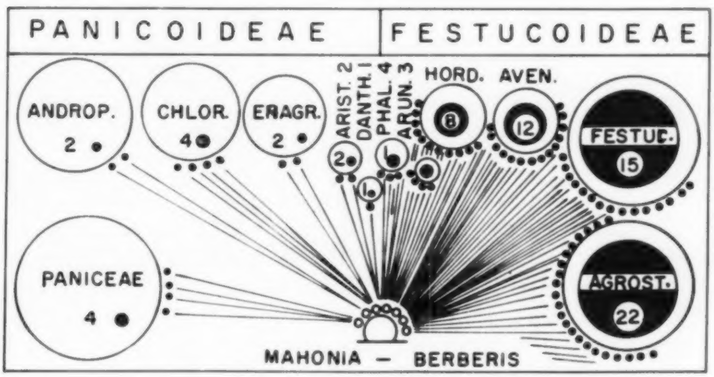

FIG. 2. Biological specialization of *Puccinia graminis* on *Mahonia-Berberis* (aecial phase: o) and on grasses (telial phase: •). White circles indicate approximate number of grass genera in a tribe, numbers in black circles host genera for the stem rust. Notice the predominance of stem rust on subfam. Festucoideae.

actually hybrids between certain species of *Mahonia* and *Berberis*. Some of these forms, for instance *Mahoberberis neuberti* (Baum.) Schneid., are highly susceptible to stem rust; some others, like *M. aqui-candidula*, *M. aqui-sargentiae* and *M. miethkeana* are known to be resistant (Cotter, **1932**).

Mahonia has about 100 living species, divided by Fedde (**1902**) into four sections. Of this number about 10 species are known to be susceptible to stem rust and many are resistant, partly because of the thickness of the cell wall of the leaves. Of the 300 living species of *Berberis* which are divided by Schneider (**1905**, **1908**, **1939**) into 21 sections, about 100 are known to be susceptible to stem rust, but not all species are yet tested (Levine and Cotter, **1932**). However, the latest (1957)

instruction of the Plant Pest Control Division of the USDA lists 56 species and varieties of *Berberis*, 3 *Mahoberberis* and 9 *Mahonia* as rust-resistant. No other genera or species of Berberidaceae are known to be inhabited by stem rust.

Such strict specialization of stem rust to a definite host sector enables us to relate the origin and phylogenetic age of this fungus to the historical development of its hosts (Leppik, **1953**, **1956**). According to this viewpoint the differentiation of stem rust as a species must have occurred at a time when the ancestral Berberidaceae had already split themselves into recent genera, but the present *Mahonia* and *Berberis* were not yet separated genetically. Existing paleobotanical findings enable us to approximate these phylogenetic events and think of the origin and evolution of stem rust in terms of the geological time, as described in a succeeding section.

On gramineous hosts numerous varieties and races of stem rust are specialized to live predominantly on the subfamily Festucoideae, and on few representatives of the subfamily Panicoideae (FIG. 2). Bambusoideae, Micrairoideae, Oryzoideae, and other tropical subfamilies of gramineous plants are not inhabited by stem rust or its close relatives. Some unequal biological specialization of stem rust races on gramineous plants depends upon the historical development of this rust mainly on the subfamily Festucoideae in the northern hemisphere in close association with barberry. It also indicates that the family Gramineae has presumably split into subfamilies before this plant group met with barberry rust. The present-day host range and biological specialization of stem rust are pictured in FIG. 2.

ANTIQUITY OF THE MAHONIA-BERBERIS ALLIANCE

We have already noted that barberry is actually the primary host and the main center of distribution of stem rust and its close relatives on gramineous plants. The early history and geographic distribution of barberry, therefore, have a particular interest in the present discussion about the origin and evolution of stem rust.

Fossil records indicate that about five species of the *Mahonia-Berberis* alliance occurred in Oligocene and Miocene of France, Italy and Switzerland (Engler and Prantl, **1891**, p. 77; Lehmann et al., **1937**, p. 45; Gothan and Weyland, **1954**, p. 391). From this material, with certainty there are identified *Berberis rhopaloides* Sap., *B. stricta* Sap., *B. aculeata* Sap., and *B. helvetica* Heer. In addition *Mahonia stenophylla* Pax is reported from the Tertiary strata of Carpathian Mountains in central

Europe, and a *Berberis* sp. from the Pliocene of Frankfurt and Sarmatia (Andreanszky and Schreter, **1959**, p. 67). These fossil species show considerable resemblance to present forms, such as *Mahonia fortunei* (Lindl.) Fedde, *M. nepalensis* DC., *M. pinnata* (Lag.) Fedde, and *M. aquifolium* Nutt., which are known to be susceptible to stem rust. Accordingly an ancestral stock of the *Mahonia-Berberis* alliance, congenial to the rust sept *Culmicola*, existed in the Old World in Eocene,

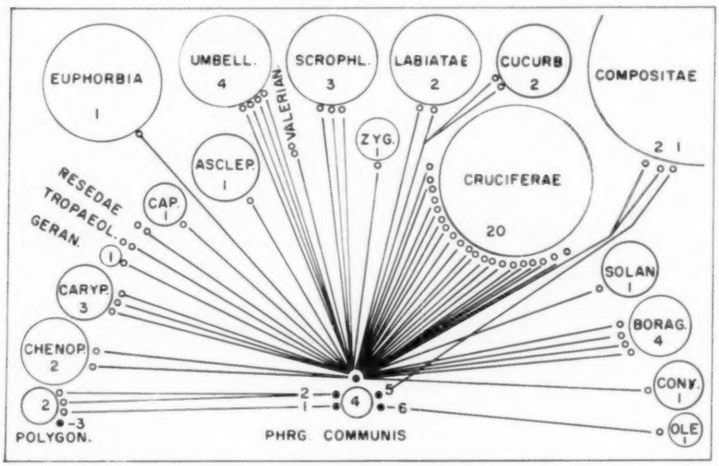

FIG. 3. Biological specialization of *Puccinia phragmitis* and related species on reed grass (telial phase: •) and higher angiosperms (aecial phase: o). 1. *P. phragmitis*. 2. *P. trailii*. 3. *P. ornata*. 4. *P. trabutii*. 5. *P. inulae-phragmiticola*. 6. *P. obtusata*.—Notice the difference between FIG. 1 and FIG. 2: stem rust has radiated from its aecial host to numerous grasses, reed rust from its telial host to many higher angiosperms.

or even earlier, although there is no trace of them from the Quaternary period anymore. At present there are no living Mahonias in Europe and only a few species of *Berberis* in the Mediterranean area. *B. vulgaris* was introduced to Europe during historical time.

A considerable number (17) of fossil species of *Mahonia* are described by various authors (Arnold, **1936**; R. W. Brown, **1940**; Axelrod, **1939**, **1956**; Chaney, **1944**; Condit, **1944**; MacGinitie, **1953**; Chaney and Axelrod, **1959**; Becker, **1959**, **1960**, **1961**) from North America. They resemble several living species that are known to be susceptible to the stem rust. Axelrod (**1956**, p. 295, Fig. 18) tried to derive some of these

species (see Fig. 4: 12–15) from *M. eocenia* Brown of the Green River flora of Eocene.

From South America (Argentina) *Berberidiphyllum reflexum* Dusen, *Berberis* sp., and *B. corymbosifolia* Berry are identified by Berry (**1938**). Whether these findings are of Eocene or early Miocene age is still under disputation (Hirmer, **1942**, p. 417, footnote, 429).

Thus many species of the *Mahonia-Berberis* alliance existed in early Tertiary, in both the Old and New Worlds, as sketched in FIG. 4. These species assumably have served as early hosts for the puccinioid rusts on barberry, including the sept *Berberidis* (see above).

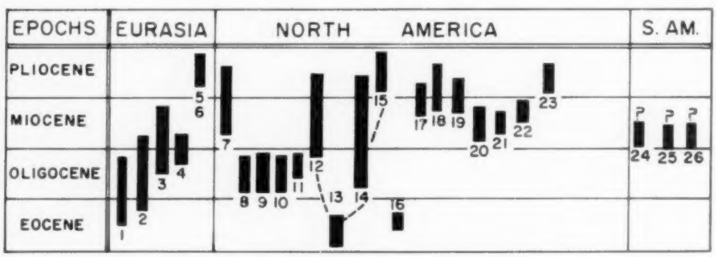

FIG. 4. Occurrence of *Mahonia-Berberis* complex in various Tertiary floras according to paleontological records. Eurasia: 1. *Berberis helvetica* Heer. 2. *B. rhopaloides* Sap. 3. *B. stricta* Sap. 4. *B. aculeata* Sap. 5. *B.* sp. 6. *Mahonia stenophylla* Pax. North America: 7. *Mahonia reticulata* (McGin.) Brown. 8. *M. obliqua* McGin. 9. *M. subdenticulata* (Lesq.) McGin. 10. *M. lobodonta* Beck. 11. *M. peloronta* Beck. 12. *M. simplex* (New.) Arnold. 13. *M. oecenia* (Brown) Arnold. 14. *M. marginata* (Lesq.) Arnold. 15. *M. creedensis* Axelr. 16. *M. hakeaeformis* Beck. 17. *M. mohavensis* Axelr. 18. *M. hollicki* (Dorf) Arnold. 19. *M. malheurensis* Arnold. 20. *M. florissantensis* (Cock.) Arnold. 21. *M. hakeaefolia* (Lesq.) Arnold. 22. *M. trainii* Arnold. 23. *M. prelanceolata* Condit. South America: 24. *Berberis corymbosifolia* Berry. 25. *B. sp.* (Berry). 26. *Berberidiphyllum reflexum* Dusen.

Since Engler (**1879**, p. 37) it is generally accepted that an extensive and uniform flora covered the northern part of Asia and North America in Eocene. Haacke (**1887**) considered the North Pole to be a creative center for the landflora and fauna general and for the complex of continents in the northern hemisphere in particular. Fedde (**1902**, p. 65) and Diels (**1942**, p. 8) assumed that the ancestors of *Mahonia* and *Berberis* might have been originally included in this circumpolar flora. During the Pleistocene glaciation, however, this flora was partly exterminated, partly broken up or driven southward by moving ice masses.

Both *Mahonia* and *Berberis* assumably migrated southwards until the present-day disjunctive areas of distribution were reached. Temporary land bridges between Arctic Asia and North America, just as between North and South America, must have favored such shifting of plants from east to west and from north to south. A similar migration of *Berberis* from Central Asia through Arabia to Ethiopia (Abyssinia) is evidenced by Diels (**1942**).

This migration theory is well supported by the phylogenetic classification of *Mahonia* and *Berberis*. Both genera are divided into two distinctive groups Septentrionales and Australes, which must necessarily have evolved in isolation.

The genus *Mahonia* is divided by Fedde (**1902**) into 4 sections, of which 3 live in North America and 1 in Asia. Schneider (**1905**, **1908**) arranged the 21 sections of the genus *Berberis* into two phylogenetically distinctive groups: 1) Eurasiatic North American, as contrasted by 2) South and Central American group. Although both these groups have developed from a common ancestral stock, they must have been evolving a long time in separation.

The genus *Mahonia* is phylogenetically older than the *Berberis*. It preferably grows in a moist warm climate, such as prevails on the Pacific coast of North America. A similar warm climate, or even warmer, presumably occurred during Eocene in the present Arctic. The more arid areas of the east coast are not inhabited by *Mahonia*. Similar climatic restrictions limit the distribution of *Mahonia* to the more maritime southeast Asia. No *Mahonia* lives at present in Europe or in Africa; no Berberidaceae exist in Australia.

The genus *Berberis* is phylogenetically younger, climatically hardier, and has a much wider distribution than *Mahonia* (Schmidt, **1929**; Rehder, **1947**). Particularly interesting is the large group of phylogenetically separated species of *Berberis* living now in Pacific South America. This group is inhabited by a number of microcyclic rusts, related to but long separated from the stem rust sept. Evidence is strong, therefore, that these rusts of the sept *Berberidis* (see above) have had similar history with their hosts, and are actually scattered remains from the early rust flora of the *Mahonia-Berberis* alliance in Eocene (FIG. 4).

EARLY ANCESTORS OF THE BARBERRY RUSTS

In previous papers the descent of aecioid rusts has been analyzed in regard to their biological specialization (Leppik, **1953**, **1956**, **1959**).

It appeared that the main evolutionary road of rust fungi lead them from the archaic fern plants over several stages on conifers and lower angiosperms up to the modern seed plants. Several aboriginal "camping-sites" and auxiliary etapes were laid on this long road, which served as centers for distribution of particular rust groups in the contemporary host sectors.

One of such posts, where the ancient rust types are well preserved, occurs on old conifers of the family Pinaceae. From this gene-center several rust families, such as Pucciniastraceae, Melampsoraceae, Cronartiaceae, Chrysomyxaceae, and Coleosporiaceae, have radiated in all directions, settling themselves on various groups of forest plants, mostly trees.

Next important center of more advanced rusts occurs on Cupressaceae. From this center the radiation of the gymnosporangioid rust types to various older orders of angiosperms, such as Rosales, Ranales, and Myricales, took place (Leppik, **1956**, p. 647). Some evidence indicates that the early ancestors of stem rust may have had the same source of origin. Several gymnosporangioid rusts on the Berberidaceae, such as *Cumminsiella, Nyssopsora,* and *Gambleola,* point to the possible common source of origin from the above-mentioned center on Cupressaceae. It is reasonable to assume, therefore, that the same center on Cupressaceae is the source of origin for the rust kin *Berberidae.*

Thus a well established sequence of host orders is demonstrated in the successive evolution of rusts from conifers to angiosperms, from trees to bushes and finally from bushes to the herbaceous plants (Leppik, **1959**, p. 520, Fig. 2). This sequence corresponds to the general differentiation of vegetation in the northern hemisphere during the Cretaceous and Tertiary periods from the conifers to the mixed forests with undergrowth, and from grassland areas to prairies and steppes as climax.

Early ancestors of stem rust, which might still have been connected with Cupressaceae, very likely disappeared under the Pleistocene glaciations together with their telial hosts. Scattered microcyclic remains of these rusts are still found on some barberry species in South America (sept *Berberidis*) and in central and southern Asia, the genus *Gambleola* on *Berberis nepalensis* (DC.) Spreng.

It is obvious that during such a mighty migration from north to south and from continent to continent, as assumably had occurred in Pleistocene, normal plant formations were broken up, and two entirely different plants, such as *Cupressus* and *Berberis* could not move together. As a matter of fact many Eocenic species of northern *Cupressus,* which might have been telial hosts for rusts, are exinct. Displaced rusts on aecial hosts, disrupted from their former telial stage, had to reduce their

heteroecious life cycle to a microcycle, or perish. Analogous destiny is expected to await our stem rust races when all susceptible barberry species could be exterminated.

There can be little doubt that the South American sept *Berberidis* is actually composed of the relics of the earlier stem rust ancestors. Morphological analogy between the septs *Berberidis* and *Culmicola* on the same host genus is too striking to deny the distant genetic relationship between these septs. But the question may be raised about the genus *Gambleola* with a single known species, *G. cornuta* Mass., on *Berberis nepalensis* in central India and China. This rust forms only spermagonia and telia on the same host. Its reduction, however, from a former puccinioid rust is quite evident. Spermagonia and spermatia of this rust are analogous with those of stem rust. Teliospores are similarly 2-celled with 2 germ pores in each cell, as those of stem rust. But since they are formed in former aecia, they are catenulate, with intercalary cells similar to these of aeciospores. Evidently this rust arose from an aecial stage of a heteroecious *Puccinia* on barberry beginning to produce teliospores in former aecia, similarly to the *Endophyllum* and other microcyclic rusts. The most plausible reason for such reduction may be the disconnection from the former telial host, possibly on some ancient *Cupresssus.*

When the contact with the aecial (or telial) host is completely lost, a fundamental change in the life cycle, accompanied by recombination in host range, occurs. There are numerous autoecious and microcyclic species among recent rusts whose origin from and a close relationship with some existing heteroecious and macrocyclic rust species are fairly evident. These microcyclic rusts, consequently, must have arisen from a heteroecious and macrocyclic ancestral stock by a recombination of their host range. But not less numerous are those examples where the aecial (or telial) phase is transferred from one host to some entirely different plant group. As a rule, the new host must be phylogenetically younger than the old host group.

It is reasonable to assume, therefore, that the sept *Berberidis* represents early relics of barberry rusts that were not connected yet with gramineous hosts. This connection might have been established during the differentiation of festucoid grasses in a close neighborhood with barbery bushes. From that point on, both the barberry and stem rust must have evolved in close connection, spreading themselves through the Tertiary period in a fast expanding grassland area of the northern hemisphere (FIG. 2).

ORIGIN AND DISTRIBUTION OF STEM RUST

There is reasonable probability that the present-day *Puccinia graminis* complex is composed of varieties and races of more recent origin than the above-discussed rusts on barberry. *Berberis vulgaris*, the main aecial host of stem rust, is obviously of Asiatic (Caucasus and Near East) origin, and has been introduced by man through Mediterranean countries to Europe, Africa and North America (Lehmann et al., **1937**). Stem rust very likely has followed its aecial host, finding everywhere a rich flora of congenial telial hosts. Large areas of grain crops and field grasses cultivated by man are particularly favorable ground for such expansion.

The present-day world-wide distribution of stem rust is very likely not an indigenous condition, but has resulted from extensive grain-growing activities of man. In Australia, New Zealand, and South Africa there are no native barberries and the stem rust is known as being introduced by man (McAlpine, **1906**; Cunningham, **1931**; Verwoerd, **1935**). According to Arthur (**1925**, p. 179), and Cortázar (**1950**), in South America there are no native species of barberry infected by stem rust. Introduced susceptible barberry occasionally exists in Chile and other South American countries. In these countries barberry is not considered as being an important source of infection for grain crops and grasses. The persistence of stem rust in these countries is due mainly to the overwintering of the uredial stage. A similar situation exists in the Union of South Africa (Verwoerd, **1935**).

In Asia, Europe, and North America barberry is of undoubted significance in the initiating of local rust outbreaks and in the process of formation of new rust strains and races (Stakman, **1918**, **1954**, **1957**; Johnson and Newton, **1933**; Hart, **1955**; Bridgmon, **1959**).

Better knowledge of the distribution of varieties and races of the stem rust complex would help to identify their centers of origin. So far the races and subraces of *P. graminis* var. *tritici* have been carefully investigated. From Johnson's (**1953**, p. 125) table it appears that China, although not adequately studied, has the largest number of races, considerably more than those in well-studied Europe and North America. Many of the Chinese races are of world-wide distribution; several are endemic. Further study may reveal a gene-center of the wheat stem rust in central Asia, the probable homeland of barberry and gene-centers of festucoid grain crops (Fig. 5).

Systematic study of stem rust collections in the United States revealed an everlasting fluctuation of races and subraces of this pathogen

in response to the host environment and climatic changes (details see: Stakman and Loegering, 1944, 1951; Stewart et al., 1959). These races are obviously of recent phylogenetic origin, because both their hosts, common barberry and festucoid grain crops, are newcomers in America.

The Asiatic origin of stem rust and its primary area of distribution in the northern hemisphere is further demonstrated in the host range of its telial stage. Almost 90 per cent of its gramineous hosts belong

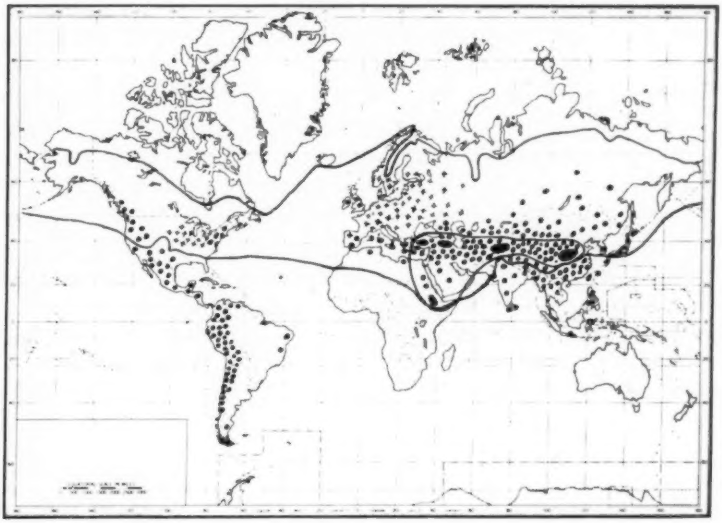

FIG. 5. World distribution of the subfam. Festucoideae (above 5% from the total amount of grasses; according to Prat, 1936). Black ellipsoids in encircled area point to the main gene-centers of cultivated Festucoideae according to Vavilow (1926, 1934). • indicates native species of *Berberis* and *Mahonia*, + the present distribution of *Berberis vulgaris*. Encircled is the area of maximum abundance of festucoid grasses, grain crops, barberries, and also the gene-center of the present-day stem rust races on cultivated grain crops.

to the subfamily Festucoideae, which has its main area of distribution in the northern hemisphere (Prat, 1936). Only very few genera of the subfamily Panicoideae, particularly those species which live in the temperate climate of the northern hemisphere, are hosts for stem rust (FIGS. 2, 5). Typical tropical and subtropical subfamilies, such as the Bambusoideae, most Panicoideae (Hartley, 1958–1960), Tripsaceae, Zoysieae, and the Danthonieae of the temperate southern hemisphere are not in-

habited by stem rust. The gene-centers of our grain crops, which are the main hosts of the present-day races, are all included in the area of the Festucoideae in the northern hemisphere (FIG. 5). This area also could be the ancestral homeland of the present-day stem rust.

SUMMARY

Available evidence indicates that the present-day *Puccinia graminis* complex is of Asiatic origin and spread in Europe, North Africa, and America together with its main aecial host, *Berberis vulgaris*. Its present world-wide distribution was obviously reached after an extensive grain crop cultivation by man.

Dominant varieties and races are those on grain crops and the present evolutionary trend of these races is toward the differentiation of newly bred improved cultivars of grain crops in different countries.

Early ancestors of stem rust were evidently of Central Asiatic origin but spread in the Tertiary through the northern hemisphere and migrated later with their barberry hosts to South America. From this rust group (sept *Berberidis*) some microcyclic relicts are left in South America and Asia, whereas some further members (sept *Phragmitis*) have established heteroecism with higher angiosperms.

ACKNOWLEDGMENTS

Acknowledgments are due to W. H. Bragonier, Head of the Department of Botany and Plant Pathology, Iowa State University, and several other persons who in one way or another helped the author to accomplish the present study. By loan from the Arthur Herbarium, J. W. Baxter, Purdue University, provided some samples of South American rusts for comparative study. Karen Heyerdahl of The Hormel Institute, University of Minnesota, assisted the author in preparing the manuscript.

Several standard illustrations of rust spores by G. B. Cummins in FIG. 1 are copied from J. C. Arthur's Manual of the Rusts (**1934**) by permission of Professor L. E. Trachtman, Executive Secretary of the Purdue Research Foundation, Lafayette, Indiana.

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NOTES ON MUCORALES, ESPECIALLY ABSIDIA [1]

C. W. Hesseltine and J. J. Ellis

(with 18 figures)

During the past few years a number of new or interesting cultures belonging to the Mucorales has been isolated at the Northern Laboratory or sent to us for identification. The media used in our studies are those reported by Hesseltine (**1954**) and Haynes et al. (**1955**).

Absidia pseudocylindrospora Hesseltine & Ellis, sp. nov.

Coloniae fuscogriseae, rapide crescentes; sporangiophora 3–6.5 μ lata, 45–172 μ longa, hyalina usque pallide brunnea, saepe in verticillis circa stolones disposita, usque 11, typice 5 in quoque verticillo; sporangia 15–35 μ, pyriformia; columellae 9–26 μ, saepe processu singulo distali praeditae; sporangiosporae 2.5 × 3.5–5 μ, cylindricae; zygosporae ignotae; chlamydosporae 8–13 μ in diam., in mycelio substrati; ad 37° C. crescens; e solo isolata.

Colonies rapidly growing, to 1.5 cm high, at 3 days Pale Olive-Gray (Ridgway Pl. 51) (**1912**) then Mouse Gray (R. Pl. 51) and after 1 month Dark Olive-Gray (R. Pl. 51); colony reverse Deep Olive-Buff (R. Pl. 40) to Pale Olive-Gray (R. Pl. 51), sometimes radially wrinkled; odor none; heavy thick colonies filling petri dishes on Czapek's solution agar; sporangiophores 3–6.5 μ in diam, 45–172 μ in length, hyaline to light brown, usually more colored next to sporangium, erect, unbranched or rarely so, arising from stolons, always with a septum below sporangium; stolons 4–16 μ in diam, smooth, occasionally septate, hyaline to pale light brown; rhizoids about 9 μ in diam, hyaline, irregularly branched, rarely septate; sporangia 15–35 μ, pyriform, many-spored, borne erect, at first white then frosty gray to olive, deliquescing, wall smooth and hyaline; columellae 9–26 μ in diam, smooth-walled except for a single projection at distal end, projections not always present, globose to somewhat hemispherical above apophysis, hyaline to light brown, well-defined collar, no contents or slightly granular material; projections on most columellae about 6 μ in length, rounded above and hyaline; sporangiospores 2.5 × 3.5–5 μ, always cylindrical or nearly so,

[1] Contribution from the Northern Utilization Research and Development Division of the Agricultural Research Service, U. S. Department of Agriculture, Peoria, Illinois.

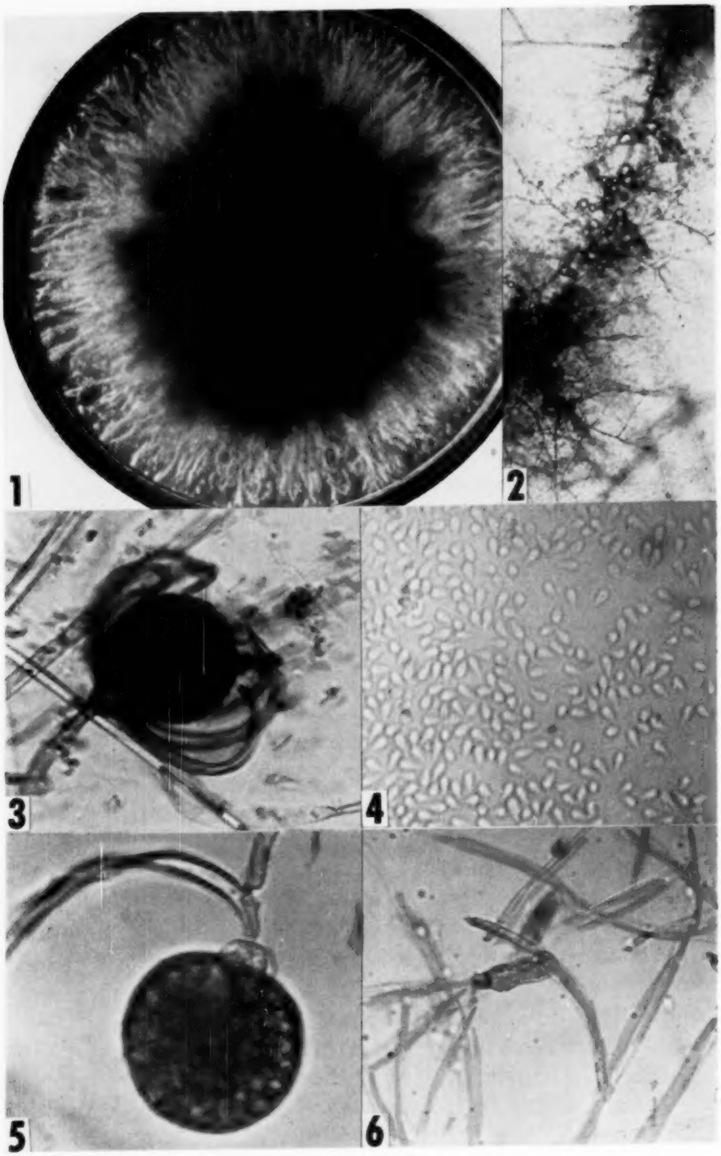
sometimes broader at one end than the other, hyaline, thin-walled, smooth, contents homogeneous; zygospores unknown; chlamydospores 8–13 μ in diam, at end of short branches of hyphae in substrate mycelium, single, globose to almost pyriform, hyaline, heavy-walled, smooth, contents granular to vacuolate; growth at 37° C.

TYPE strain: NRRL 2770. This strain was isolated by Dr. A. W. Poitras from soil in British East Africa collected by A. Woehrl with the notation "Kilema alt. 4500, virgin subsoil, April 1953."

The description given above was prepared from studies of the type strain on synthetic mucor agar (SMA) at 25° C at about 7 days of age. Growth at 37° C on potato dextrose agar (PDA) at 14 days had restricted colonies approximately 5 cm in diam with aerial mycelium and sporangia. The reverse is wrinkled and Buffy Brown (R. Pl. 40). On Czapek's solution agar, this species is distinct from other species of *Absidia* in that it produces a heavy dark colony which fills the entire petri dish. Sporulation is excellent on this medium. On malt extract agar the colonies have about the same appearance as on SMA, except the reverse is smooth and pale brown in color and the amount of mycelium is not so great. Fruiting begins in 72 hours on this medium and others. On PDA, good growth and sporulation occur with the reverse of the colonies grayish colored and white at point of inoculation.

Since the manner in which the sporangiophores, stolons and rhizoids are arranged cannot be seen too clearly on SMA, the following description is based on studies of this species on hay agar at about 9 days where these structures may be readily seen. On this medium fruiting is excellent. Some sporangiophores may be branched, but usually they are simple. Sometimes the sporangiophores are arranged singly along the stolons, but none are ever opposite the rhizoids. More typically, the sporangiophores are in whorls. The typical number is 5 but some have been seen with 7 arranged like spokes of a wheel from the stolons. In rare cases as many as 11 have been seen in a single whorl. The stolons are arched with the sporangiophores arising in the arch; at the points where they touch the agar, rhizoids are formed. A short distance above this point a new arch is formed, and this pattern of growth goes on indefinitely and results in all the aerial mycelium being fertile.

Because of its cylindrical spores, this species is closely related to *A. cylindrospora* Hagem. The type culture of *A. cylindrospora* deposited in the Baarn Collection many years ago is available in our collection for comparison as NRRL 2796. *A. pseudocylindrospora* differs from *A. cylindrospora* in the following ways: (1) Growth is extremely heavy and luxuriant on Czapek's solution agar. (2) Some growth and considerable



FIGS. 1–6.

sporulation occur at 37° C on SMA although the colonies do not cover the plates or fill the dish as they do at 25° C. No growth of *A. cylindrospora* occurs at this temperature. (3) Colonies are much darker in color. (4) The whorls have more sporangiophores than do those of *A. cylindrospora*, which typically has only 4 or less. (5) The sporangiophores are shorter in length. (6) No zygospores were ever found in the mating of *A. pseudocylindrospora* and a number of sets of mating cultures of *A. cylindrospora*.

ABSIDIA CYLINDROSPORA var. **rhizomorpha** Hesseltine & Ellis, var. nov. FIGS. 1–3

Coloniae rapide crescentes, griseae, massas radiantes mycelii albi rhizomorphis similes in substratis nonnullis gerentes; sporangiophora, sporangia et columellae eis speciei *A. cylindrophorae* similia; sporangiosporae 2.2–3.3 × 3.3–6.5 μ, e cylindricis usque fere cuboideae; zygosporae 26–78 μ, globosae, atrobrunneae; processus digitaliformes e suspensoribus zygosporas circumdati; species heterothallica; ad 37° C. crescens; e solo ad rhizosphaeram *Musae* adsociata.

Colonies rapidly growing, to 1.5 cm in height, Light Gull Gray (R. Pl. 53) to Pale Olive-Gray (R. Pl. 51), at one month near Light Olive-Gray (R. Pl. 51); colony reverse wrinkled radially and Pale Olive-Buff (R. Pl. 40); to Olive-Buff (R. Pl. 40) at one month, with margins lighter in color, on Czapek's solution agar growth abundant and luxuriant with margin of colony showing radiating masses of white mycelium resembling rhizomorphs; odor none; sporangiophores 2–8.6 × 90–310 μ, formed tardily, arising from stolons, smooth-walled, with a septum under each sporangium, erect, hyaline to brown, typically undivided but occasionally branched, sometimes arising singly, others arranged in whorls of 2–4, very rarely 5; stolons 5–20 μ in diam, sometimes septate, but not septate at origin of sporangiophores, smooth, hyaline to light tan to brown, forming extensive mycelium when they touch the agar; sporangia 26–47 μ in length and 20–42 μ in diam, pyriform, multispored, deliquescing, at first white then in reflected light tan to dark olive, with a well-defined apophysis; sporangial wall smooth, transparent; columellae 12–36 μ in diam, nearly spatulate, globose to applanate, smooth, without a terminal projection, hyaline to light brown, collar sometimes present, contents empty; sporangiospores 2.2–3.3 × 3.3–6.5 μ, cylindrical, almost dumbbell-shaped to nearly cubical, smooth, hyaline, with granular material

FIGS. 1-6. 1. *Absidia cylindrospora* var. *rhizomorpha* (NRRL 2771), showing rhizomorphic growth on Czapek's solution agar, × ¾. 2. A rhizomorphic strand of *A. cylindrospora* var. *rhizomorpha*, × 150. 3. *A. cylindrospora* var. *rhizomorpha* zygospore, × 300. 4. Sporangiospores of *Gongronella lacrispora* (NRRL 2643), × 350. 5. Sporangium of *G. lacrispora* showing hemispherical apophysis, × 650. 6. *G. lacrispora* × *G. butleri* (NRRL 1308), showing gametangial fusion, × 325.

typically at each end; swollen cells to 20 μ in diam formed at ends of substrate hyphae, thin-walled, regularly globose, abundant, solitary and empty and not separated by a septum from the hyphae; substrate mycelium irregular in size, hyaline and filled with colorless oil droplets; no oidia or chlamydospores; zygospores 26–62 μ (on hay agar from 52–78 μ) but average near 52 μ, always globose, borne between unequal suspensors, with exudate surrounding zygospore, blackish-brown, always scattered in a diffuse manner in the aerial portion of colony, roughened with short spines; spines of zygospores stellate, from 2–4 μ in length; larger suspensors same size as aerial hyphae but with a globose to pyriform swelling next to zygospore to 20 μ in diam, smooth, brown, with fingerlike projections from swollen region of suspensor which encloses zygospore; fingerlike projections up to 6.0 μ in diam, number up to 10, typically unseptate, slightly roughened at their base, heavy-walled, dark brown, rigid, with ends blunt; smaller suspensor not swollen, without projections; heterothallic; growth at 37° C.

TYPE: NRRL 2771, isolated by Dr. R. D. Goos, United Fruit Company, from banana rhizosphere soil, obtained at La Lima, Honduras in July 1958. Two other isolates from the same source as NRRL 2771 were received from Dr. Goos; one of these, designated NRRL 2815, proved to be the opposite mating type.

The description above is based on a study of the 3 strains grown on SMA for 6–18 days at 25° C. At 10 days fruiting typically has just begun although the colonies filled the petri dishes. In reverse the colonies are wrinkled and Pale Olive-Buff (R. Pl. 40) in the center, but the margins are grayish tinted. The arrangement of the sporangiophores was described from hay agar. The zygosporic stage was studied on PDA and hay agar at 25° C. Even though zygospores form on a variety of media, they were never very abundant in our strains.

On PDA plates, colonies of this *Absidia* are light grayish brown and within 6 days a few sporangia are seen. Growth and sporulation are excellent on this medium; the agar is covered and the dish filled with mycelium. The reverse is white with a wavy zonation. On malt extract agar this species has the same general appearance as on PDA.

On Czapek's solution agar at 6 days, colonies cover the agar in petri dishes, have light gray centers and reach the lid of the dishes. The colony margins are white with little aerial growth and show white rhizomorphlike strands radiating to the edge of the dish. The rhizomorphlike growths are composed of large hyphae with numerous swollen cells and from the large hyphae radiate mycelium that is extremely small in diameter. The colony reverse is white to cream-colored, wrinkled, with the

rhizomorphlike structures clearly visible. At about 1 month, the cultures have a darker reverse near Olive Brown (R. Pl. 40) to Clove Brown (R. Pl. 40). On this medium sporulation occurs after a week.

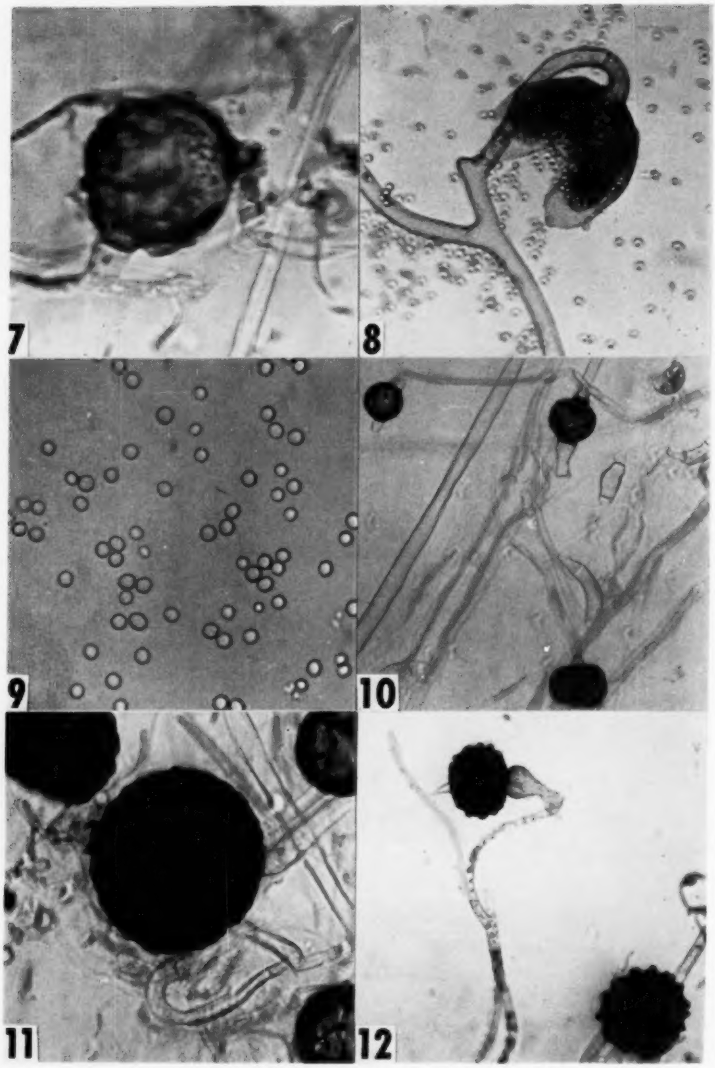
The zygosporic stage was readily obtained when NRRL 2771 and NRRL 2815 were mated on appropriate media such as PDA or hay agar. The zygospores are formed in a diffuse fashion in the aerial mycelium portion of the colony. The suspensor, bearing the long fingerlike projections surrounding the zygospores, is narrow, except next to the zygospore where it enlarges as a globose to pyriform swelling. The fingerlike projections develop from this large swelling. The small suspensor is not swollen and does not have projections on it. At least in some cases, the suspensors are borne on stolons, which have sporangiophores. Often the filament that bears a suspensor is extended a short distance as a sterile spine.

This variety differs from *A. cylindrospora* by showing (1) rhizomorphic strands of hyphae, (2) luxuriant growth on Czapek's solution agar and good growth at 37° C and (3) failure to mate with various mating types of *A. cylindrospora*.

Gongronella lacrispora Hesseltine & Ellis, sp. nov. FIGS. 4–7

Coloniae tarde crescentes, 1–3 mm altae, vinaceae; sporangiophora usque 6.5 μ in diam. e substrato enata, erectae, ramosae, ramis 30–90 μ sporangia circinate vel circulariter gerentibus; sporangia 13–41 μ in diam., globosa, apophyse hemisphaerica praedita; columella 2.5–13 × 4.5–20 μ dorsiventraliter applanata vel sphaerica, glabrotunicata, collare ornata; sporangiosporae 2.8–4.5 × 5.5–9 μ, lacrimoideae, hyalinae, tunica extremum attenuatum versus incrassata; chlamydosporae 8.5–11 μ in diam., in mycelio substrati; species heterothallica; e solo isolata.

Colonies slow growing, 5 cm in diam in 13 days, 1–3 mm high, thickly floccose to felty, margin irregular, at first white then Pallid Neutral Gray (R. Pl. 53) or Pale Olive-Gray (R. Pl. 51), later Pale Vinaceous-Drab (R. Pl. 45), Pale Vinaceous-Fawn (R. Pl. 40), to Light Vinaceous-Fawn (R. Pl. 40) and Vinaceous-Buff (R. Pl. 40) toward the center of colony and at 1 month Drab Gray (R. Pl. 46), hence with a definite vinaceous or pink shade; colony reverse Pale Olive-Buff (R. Pl. 40) to Deep Olive-Buff (R. Pl. 40) at 1 month, wrinkled and furrowed both radially and circularly which also appears on surface of colonies; odor none to slight; sporangiophores up to 6.5 μ in diam, from substrate and erect, smooth to very minutely roughened, rarely septate, multisporangiate, with the larger sporangia below, bearing one sporangium at a place, often terminated by a sterile filament; nonphototrophic; branches 30–90 μ in length, bearing sporangia circinately to circularly, with the continua-



FIGS. 7–12.

FIGS. 7–12. 7. *Gongronella lacrispora* × *G. butleri*, showing imperfect zygospore, × 325. 8. Sporangium of *Circinella angarensis* (NRRL 2410), × 325. 9. Sporangiospores of *C. angarensis*, × 650. 10–11. Young and mature zygospores of *C. angarensis*, × 325 and × 650, respectively. 12. Zygospores of *Zygorhynchus macrocarpus* (NRRL 2663), × 325.

tion of the sporangiophore arising in the upper portion of the circle and often constricted at this point, branches bearing sporangia constricted below apophyses, easily fractured 20–40 μ below sporangium; often with septa in upper region of the curvature; rhizoids and stolons absent; sporangia 13–41 μ in diam, typically perfectly globose, at first white, then grayish olive and in age with a yellow to tan tint in reflected light, multispored, always borne circinately, always with an apophysis, sometimes abortive sporangia present; sporangial wall smooth, thin, transparent, fragile; apophyses 4–8.6 μ in diam, hemispherical, hyaline, smooth; columellae 2.5–13 × 4.5–20 μ, dorsiventrally flattened to spherical, smooth-walled, hyaline, with a collar always present, often constricted at attachment to apophyses; sporangiospores 2.8–4.5 × 5.5–9 μ, lacrimoid to narrowly napiform, hyaline, light yellow brown in mass, thick-walled especially at the tapered end, smooth; sporangiospore contents hyaline to light buff, finely granular; chlamydospores to 8.5 × 11 μ, borne in great abundance in substrate mycelium, usually simple and terminal, typically globose but also oval, smooth, contents granular and vacuolate; giant cells from 20–37 × 60 μ, in substrate mycelium, hyaline, globose to irregular, intercalary, often with large vacuoles or oil droplets; zygospores unknown; heterothallic.

TYPE: NRRL 2643. Isolated by C. W. Emmons, National Institutes of Health, from a dooryard soil sample, Clarksburg, Maryland.

The preceding description is based upon NRRL 2643 growing on SMA at 25° C at 13–16 days unless otherwise noted. Eight other strains were studied from the same source, but each was practically identical with NRRL 2643. At 6° C no growth occurred in 20 days; at 14° C colonies in 13 days were 20 mm in diam, with thick, moist, matted growth having a few aerial hyphal tufts and no sporangia; growth at 37° C was low, thick, very wrinkled and with sporangia.

G. lacrispora, when grown on PDA, showed excellent growth and sporulation, but the colonies never covered the surface of the agar. The colonies had a pale vinaceous color and were more floccose in appearance and less matted. The same chlamydospores and giant cells were present. Malt extract agar gave about the same type of color and growth as with PDA. At 25° C colonies on Czapek's solution agar for 24 days were very matted and had thick growth, but they did not cover the surface of the agar. Sporangia were very numerous. The reverse of the colony was wrinkled, and chlamydospores and giant cells had been formed in abundance.

All strains were mated in various combinations but no zygospores were obtained.

G. lacrispora shows only one characteristic of the genus *Circinella;* the sporangia are always borne circinately. Even this characteristic is somewhat different in that the sporangium, instead of being borne in a circinate or bent fashion, is borne at the end of almost a complete circle. It differs from species of *Circinella* in the following respects: (1) Sporangiospores are regularly teardrop-shaped. The sporangiospores have a thick wall that includes the tapered portion of the teardrop (FIG. 4); whereas the broad region of the spore shows a heavy wall, a lighter homogeneous zone and a central granular and vacuolated region. The whole sporangiospore appears somewhat like the sporangium of *Bacillus,* which contains one spore. (2) The fragile sporangiophores break as readily as does spun glass. (3) A hemispherical apophysis invariably occurs beneath the sporangium, which resembles the apophysis of *Gongronella butleri* (Lendner) Peyronel & Dal Vesco (**1955**) (*Absidia butleri* Lendn.). We regard this third feature to be of considerable generic importance, and it clearly is not characteristic of the genus *Circinella.*

As noted, *G. lacrispora* grows luxuriantly on Czapek's solution agar, a medium not found to support good growth of most mucors, including all species of *Circinella.* Similarly, *G. butleri* grows quite well on this medium. Likewise, colonies of both *G. butleri* and *G. lacrispora* grow slowly, reach only a few mm in height and are nearly the same color. As far as is known, both species are strictly soil forms. However, none of these characters alone would justify placing this species in the genus *Gongronella.* Since we failed to obtain any zygospores by mating the available strains, they were mated with our strongest mating types of *Circinella muscae* (Sorokine) Berl. & de Toni on media appropriate for zygospore formation for *C. muscae.* Although on such media as yeast extract soluble starch agar (YPSS) there seemed to be stimulation of growth of both plus and minus strains of *C. muscae,* no imperfect reaction of any sort could be detected even with repeated matings. It then occurred to us that we should attempt matings with *G. butleri.* When NRRL 2643 was mated on PDA at 25° C with mating types of *G. butleri,* NRRL 1307(+) and NRRL 1308(−), the reaction with NRRL 1307 was negative but a strong and immediate mating reaction occurred with NRRL 1308. This reaction indicated that NRRL 2643 was (+). Subsequent mating of all the other strains of *G. lacrispora* gave the same mating reaction with NRRL 1308 and were negative with NRRL 1307, indicating that all isolates of this species were (+) in reaction and that the species was indeed heterothallic. It was apparent that this new species was closely related to *G. butleri.* For this and the reasons given above, we have placed this new species in the genus *Gongronella,* which

Ribaldi (**1952**) proposed. It therefore becomes necessary to enlarge our concept of *Gongronella* to include forms without stolons—*Gongronella* has very few and poor rhizoids and stolons—and also to include forms that have their sporangia borne circinately. The hemispherical-shaped apophysis, on the other hand, assumes great generic importance.

The imperfect reaction between *G. lacrispora* and *G. butleri* has been followed in some detail. When NRRL 1308(−) and NRRL 2643 are mated on PDA, the rates of growth are strikingly different; NRRL 1308 (*G. butleri*) grows up to NRRL 2643 and then almost surrounds it. Zygospores are formed only at some places where the two colonies come into contact and not as a solid dark line of zygospores, readily visible macroscopically, as occurs when compatible strains of *G. butleri* are placed together.

In certain regions after contact of the colonies of the compatible strains of *G. butleri* and *G. lacrispora*, progametangia are formed in the aerial mycelium slightly above the substrate. Progametangia come into contact, fuse and remain parallel to each other. The fusions may be in a ladderlike fashion, or one filament may form a progametangium at its end and fuse with a progametangium arising from the side of the zygophore of the opposite mating type.

Although many fusions occur, still only a very few zygospores develop. When cultures are mature, a few zygospores can be found. They are yellow brown, varying from nearly smooth to verrucose and globose. The projections on the zygospores are blunt and about $2\,\mu$ in length. The zygospores measure from 17–$26\,\mu$ in diam as contrasted to normal *G. butleri* zygospores which reach a size of $37\,\mu$, are more roughened and assume a darker brown color.

The suspensors formed in the imperfect reactions between NRRL 2643 and NRRL 1308 are parallel to each other, hyaline and smooth, and measure from 7–$13\,\mu$ in diam. The zygophores are hyaline, thin-walled and sometimes minutely roughened, and measure about 4–$5\,\mu$ in diam.

CIRCINELLA ANGARENSIS (Schost.) Zycha. Kryptogamenflora Mark Brandenburg **6A**: 98. 1935. FIGS. 8–11

Mucor angarensis Schost. Ber. Deut. Bot. Ges. **15**: 473. 1897.

Colonies up to 1.5 cm in height, vigorously growing but never covering all the surface of the agar, with sporangial colonies, at first white then Light Drab (R. Pl. 46) to Cinnamon Drab (R. Pl. 46) or Buffy Brown (R. Pl. 40), never showing gray as an intermediate color; colony reverse Light Drab (R. Pl. 46) to lighter at the irregular margin; odor

none; sporangiophores to 1.5 cm in height and to 35 μ in diam, brown, with droplets of exudate, erect to prostrate, from substrate, granular appearing or even striate at higher magnification, sympodially branched, bearing sporangia on circinate branches or occasionally with sporangia borne erect, with 1 or 2 sporangia to a branch, often with a spine or a suggestion of a spine, sporangia also on simple branches; branches with 1–5 septations below the sporangium, brown, to 300 μ or more in length; spines may often occur singly or with a sporangium, often but not always delimited by a septum, brown colored, terminal end blunted, not pointed as in *C. muscae*; rhizoids and stolons absent; sporangia up to 205 μ in diam, at first white then light brown to buff in reflected light, blackish in transmitted light; sporangial wall breaking at the dorsal surface and opening like a *Geaster*, incrusted, granular, hyaline with the spores clearly visible inside; columellae 30–124 × 65–154 μ, hyaline to light brown with granular wall, cylindrical, pyriform, oval or globose, with spines on the smaller columellae, with a pronounced collar or even large fragments of the sporangial wall attached; sporangiospores 6–13 μ in diam, contents uniform, often showing a double wall, smooth, thin-walled, globose to very short oval; chlamydospores, oidia missing; zygospores 30–70 μ in diam, appearing as a dark, narrow line across plate, formed at the surface of the agar or 1–2 mm above surface of agar, thick-walled (5 μ), slightly roughened or verrucose in outline as viewed from the surface, striate, with striations converging on the thickened areas of the zygospore wall, globose to nearly so, smaller ovoid, yellow brown to brown in color with a large, single, oil droplet; suspensors 12–27 μ in diam, equal, parallel or nearly so, hyaline to light yellow brown, smooth; zygophores up to 8 μ in diam, thin-walled, hyaline, smooth, with zygospores arranged at right angles, with a sterile spinelike terminal end above suspensor; heterothallic; growth and sporulation at 37° C.

TYPE: Since the original material upon which Schostakowitsch based his study is probably no longer in existence, we propose NRRL 2410, as the NEOTYPE.

The description above was prepared from a study of NRRL 2410 on SMA at about 9 days at 25° C, except for the zygospores which were observed at 25° C on corn steep liquor and YPSS agars. On PDA and malt extract agar, growth is excellent and the colonies are brown. In old cultures large numbers of short, small sporangiophores arise from the substrate mycelium that bears many simple branches ending in a small sporangium, each of which is borne circinately.

Circinella angarensis grows readily on most media commonly used for the study of Mucorales. The two isolates available for study appear to be almost identical and therefore the description of the growth of the species on SMA is based on strain NRRL 2410(+). This strain was

isolated by R. K. Benjamin from dung collected by D. H. Ford, Angeles Crest Highway, San Gabriel Mountains, Calif., Nov. 20, 1953. The second strain NRRL 2628(−), which mates with NRRL 2410, was isolated from a rodent dung sample collected by one of us (CWH) from the San Gabriel Mountains near Claremont, Calif., in Sept., 1957.

When NRRL 2410 is mated with NRRL 2628 at 25° C, fusions of the gametangia are observed in 3 days on the surface of the agar and others are seen a short distance above the surface of the medium. The suspensors are not coiled about each other but are usually arranged in a parallel fashion as seen in *C. muscae*. At 3 days a white line can be seen at the region where the two strains have come in contact, and the colony reverse shows a light yellow line. The rates of growth of the two strains are about the same. As the culture becomes older, the narrow yellow line across the plate turns dark brown.

Zygospores are produced in abundance on YPSS, tomato paste-oatmeal agar (TPO) and PDA. On malt extract agar some zygospores are formed but not as abundantly as on YPSS and the line of zygospores is not visible macroscopically. On YPSS enormous numbers of small sporangia are found on short sporangiophores. A few zygospores can be seen on hay agar.

Schostakowitsch (**1897**) reported *C. angarensis* from goat dung from Irkutsk, Siberia, and noted that it was a rare species. Although he placed it in the genus *Mucor,* he stated that it had similarities to the genus *Circinella*. Zycha (**1935**), who saw no material of the species, removed the species from *Mucor* to *Circinella* on the basis of the data given by Schostakowitsch. Our isolates agree remarkably well with Schostakowitsch's description and with the three figures used by him to illustrate the species. The species belong with absolute certainty in the genus *Circinella* because of (1) circinate sporangia, (2) the *Circinella*-type zygospores with parallel suspensors as in *C. muscae,* (3) persistent sporangial walls, (4) the occurrence of sterile spines on the sporangiophore, (5) the same type of columellae as seen in other species of *Circinella,* (6) the nearly globose sporangiospores like those in other species of *Circinella* and (7) imperfect mating between this and the mating strains of *C. muscae*. It may be recognized among all other species of *Circinella* by the robust nature of its sporangiophores and the sporangiospores, which are larger in dimension than those of any other species of *Circinella*.

This species does show some definite *Mucor*-like characteristics, including slight roughening of the zygospores, the occurrence of zygophores bearing zygospores aerially above the medium, parallel and equal sus-

pensors and some sporangia borne practically upright. One might postulate that from an ancestorial *Mucor* with persistent sporangial walls arose *C. angarensis,* which in turn gave rise to *C. muscae,* which in turn produced such advanced forms as *C. umbellata* with umbels of sporangia and with smooth-walled zygospores borne on the surface of the medium between tong-shaped suspensors.

The mating reaction type of the two cultures was established by crossing each strain with *Circinella muscae* mating types previously reported by Hesseltine and Fennell (**1955**), namely NRRL 1359(+) and NRRL 1358(−). The mating reaction of these strains had been determined many years ago by Blakeslee. When NRRL 2628 was mated with *C. muscae* NRRL 1359(+) on corn steep liquor agar at 25° C, a good positive reaction occurred and a few gametangial fusions produced zygospores, which were about 35 μ in diameter, in 14 days on YPSS. The first fusions of progametangia were seen in 72 hours. This combination even showed some yellow orange pigment where the strains came into contact and some brown zygospores were formed. The other combination, NRRL 2410 × *C. muscae* NRRL 1358(−), showed some gametangial fusions but the mating reaction on corn steep liquor agar and YPSS did not produce any imperfect brown zygospores. Our work established the mating types in *C. angarensis* and showed that the species was related to *C. muscae.*

The zygospores of Zygorhynchus macrocarpus. FIG. 12

At the time the genus *Zygorhynchus* was monographed by Hesseltine, Benjamin, and Mehrotra (**1959**) they had available only one strain of *Z. macrocarpus* Ling-Young, NRRL 2663. They had considered it as still possibly representing the type strain even though no zygospores were encountered in their study. Nevertheless, Ling-Young (**1930**) had reported zygospores when she described the species. Later the same strain was obtained from Mr. E. V. Crisan of Purdue University, which had likewise come from the Baarn Collection as did our strain but which had been carried for several years in the Purdue Culture Collection. A study of the Purdue strain led to the discovery of zygospores both in it and in NRRL 2663. Since the two strains are identical in appearance, we are sure they represent Ling-Young's original type culture. When NRRL 2663 is placed on PDA and incubated for about 2 weeks at 15° C, numerous typical *Zygorhynchus* zygospores are formed. At this temperature zygospores can be obtained on SMA, Czapek's solution agar and malt extract agar and, presumably, on many other media.

However, the largest number of zygospores are produced on PDA. An occasional zygospore will be formed on PDA at 20° C, but this temperature is definitely too warm for the normal production of zygospores. The following description of the zygospores is given:

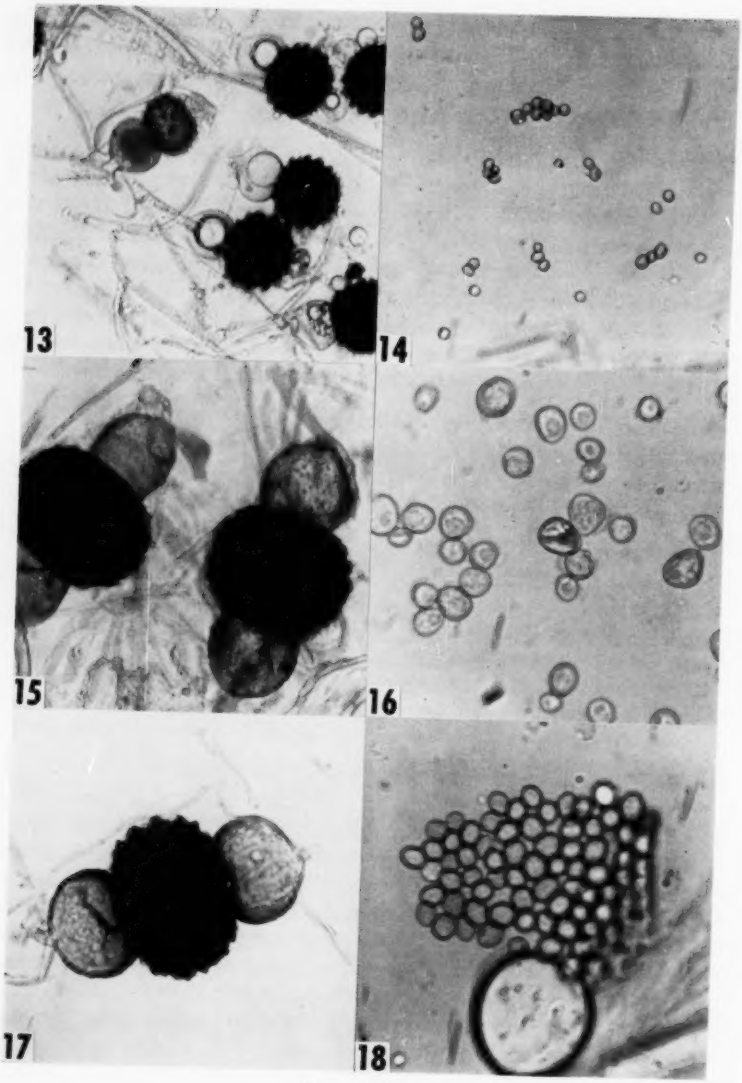
Zygospores 40–80 μ in diam, globose to compressed between suspensors, invariably black when mature, scattered through the aerial portion of colony, roughened with spines, borne between unequal suspensors; spines on zygospores 4.5–6.5 μ in length and to 10 μ in width at base, stellate, blunt, sometimes recurved; large suspensors roughened, long, recurved, abruptly swollen near the zygospore, swollen region 28–37 μ in diam and filled with yellowish granular material or oil droplets; smaller suspensor, short, 8–10 μ in length and 6–8.6 μ in diam, hyaline, straight; homothallic; forming zygospores at temperatures below 20° C.

Our earlier recognition of this species of *Zygorhynchus* has been confirmed and we believe that, undoubtedly, strain NRRL 2663 is the type strain of the species.

Rhizopus homothallicus Hesseltine & Ellis, sp. nov. FIGS. 13–14

Coloniae rapide crescentes, griseae; sporangiophora 5–30 μ in diam., usque 2000 μ vel magis longa, saepe quidem infra sporangia dichotome ramosa; sporangia 26–140 μ in diam., globosa, atrogrisea; columellae 14–67 × 18–72 μ; sporangiosporae globosae, 4.5–8 μ vel breve ovoideae, 3.5–5 × 4.5–7 μ, substriatae; chlamydosporae 15–36 μ in diam.; zygosporae 40–140 μ, typice 60–90 μ, globosae, brunneae, processibus 8 μ longis ornatae; suspensores inaequales, alius inflatus, longus et inflexus, alius rectus brevisque; species homothallica; ad 37° C. bene crescens; e solo isolatus.

Colonies on SMA at first white with sterile aerial mycelium, rapidly covering the agar in petri dishes, at 2 weeks colonies Pale Smoke Gray (R. Pl. 46), Light Grayish Olive (R. Pl. 46) or Smoke Gray (R. Pl. 46), reaching a height of 1 cm; colony reverse at this age Light Mineral Gray (R. Pl. 47) to Pale Olive Gray (R. Pl. 51), sometimes zonate like *Mortierella* colonies; in old cultures colonies remaining gray and not changing color in reverse; odor none; sporangiophores 5–30 μ in diam (more details on Czapek's solution agar are given below) and at least 2000 μ in length for those not originating opposite rhizoids, others opposite rhizoids on stolons, or from stolons without rhizoids, never abundant in numbers, sometimes near the rim of petri dishes, hyaline to brown but part of sporangiophore always brown, not septate, smooth-walled or granular or pitted, often branched dichotomously just below the sporangia but unbranched below; sporangia 26–140 μ, borne erect, globose, blackish gray in reflected light, apophysis black and conspicuous; sporangial wall incrusted, transparent, breaking; columellae 14–67 × 18–72 μ but a few to 78 × 83 μ, nearly globose or slightly wider than long



FIGS. 13–18.

FIGS. 13–18. 13. Zygospores of *Rhizopus homothallicus* (NRRL 2538), × 125. 14. Sporangiospores of *R. homothallicus*, × 250. 15. Zygospores of *Rhizopus sexualis* (NRRL 2567), × 125. 16. Sporangiospores of *R. sexualis*, × 250. 17. Zygospore of *Rhizopus sexualis* var. *americanus* (NRRL 2626), × 125. 18. Sporangiospores of *R. sexualis* var. *americanus*, × 250.

in larger ones, smaller spatulate to very short oval, light gray to light grayish-brown, smooth-walled, collar present in some cases, appearing empty or with oil droplets and granular material; sporangiospores quite regular in size, 4.5–8 μ in diam for globose spores, 3.5–5 × 4.5–7 μ for very short oval spores, occasionally slightly angled, contents uniform or with small droplets; sporangiospore wall rather heavy, gray in color singly, smooth, but marked with faint striations; chlamydospores 15–36 μ in diam, intercalary, solitary, smooth-walled, hyaline, thick-walled, subglobose, oval, cylindrical to irregular; zygospores 40–104 μ in diam, typically 60–90 μ in diam, globose or slightly compressed between suspensors, bright brown to dark yellow brown, scattered throughout aerial mycelium, covered with projections; projections of zygospores to 8 μ in length and to 10 μ in width at base, stellate, blunt or pointed at their ends, with projections sometimes bent at their ends; suspensors unequal, hyaline to golden yellow or light brown next to the zygospore, typically empty; zygospores borne between a long bent suspensor and a very short one as in *Zygorhynchus*; large suspensor nearly globose next to the zygospore and abruptly tapering down to the narrow sometimes roughened portion of suspensor which varies from 4–10 μ in diam, the swollen region from 32–70 μ in diam; smaller suspensors 20–36 μ in diam, smooth, hyaline to light brown, short, straight, often with a roughened unbranched filament extending above the origin of the smaller suspensor and often cut off with a septum; homothallic; good growth and zygospore formation at 37° C.

TYPE: Strain NRRL 2538 isolated from a soil sample collected in 1956 by Dr. R. W. Jackson in Guatemala at Zacapa Station, 280 km northeast of Guatemala City in a tropical desert with only 13 inches of rainfall annually. A second isolate was sent to us in 1961 by Professor J. N. Rai, Microbiology Laboratory, University of Lucknow, Lucknow, India, and is carried as NRRL 2935 in our collection.

The description is based on studies of the 2 strains grown on SMA at 25° C for about 2 weeks. Only 2 strains of this species have ever been found. They differ slightly in morphology. NRRL 2538 produces more and somewhat larger sporangia (60–140 μ), while those of NRRL 2935 range from 26–94 μ. The columellae of NRRL 2538 appear slightly brown, the other tends to have a gray tint. The number of chlamydospores varied from very few in NRRL 2538 to many in NRRL 2935.

Additional information concerning some structures was obtained by study of our strains on Czapek's solution agar at 25° C where growth is very thin and sparse but where all stages of the fungus develop, including zygospores. Sporangiophores are 400–800 μ in length when

opposite rhizoids, brown in color and as many as 4 arise from one place. Such a group is exceptional since only a single sporangiophore is typical. The stolons are hyaline to faintly colored, smooth to roughened and up to 14 μ in diam. The rhizoids are brown in color, fading to hyaline at their tips, branched, sometimes septate, smooth, up to 11 μ in diam and 220 μ in length. Chlamydospores are seen in the substrate mycelium, globose to oval, smooth, hyaline, single, intercalary, 10–26 μ in diam with a dense granular or vacuolate cytoplasm.

Colonies on PDA grow luxuriantly and produce large numbers of sporangia and zygospores. They are gray and appear like typical *Rhizopus* colonies. As the cultures become old, the colonies assume a slightly brownish color with the reverse in yellow tints. Growth at 37° C is very good with zygospores, sporangia and chlamydospores.

Chlamydospores are seen in greater abundance on PDA in the aerial mycelium but have the size and appearance as described above. In old cultures chlamydospores on this medium are extremely abundant in the aerial mycelium.

Growth on malt extract agar is similar to that on PDA but the colonies are lower (3–4 mm) at both 25° and 37° C.

Zygospores appear in cultures by the 4th day. They arise from a branch of a filament growing outward and then bending inward to come into contact with a very short straight progametangium in a fashion reminiscent of *Zygorhynchus.* The longer suspensor always is the one that is swollen abruptly and has the larger diameter. In every case where zygospore formation could be traced, the formation occurred in this manner.

Rhizopus homothallicus is near the presumably heterothallic species *R. arrhizus* Fischer, but possesses smaller, nearly globose spores with less clearly defined striations and is homothallic. The only other homothallic species of *Rhizopus, R. sexualis,* has much larger sporangiospores (reported to 18 μ in length), does not grow at 37° C and has suspensors nearly equal in size. For comparison, the following description is given of the type strain of *R. sexualis* (Smith) Callen.

RHIZOPUS SEXUALIS (Smith) Callen, Ann. Bot. N. S. **4**: 793. 1940.
FIGS. 15–16

Mucor sexualis Smith, Brit. Mycol. Soc. Trans. **22**: 252. 1939.

Colonies on SMA rapidly growing, covering the agar in petri dishes in 5 days at 25° C, grayish colored with areas of white mycelium and much sterile aerial mycelium, to 0.5 cm high, Light Olive-Gray (R. Pl. 51), at one month Light Grayish Olive (R. Pl. 46); colony reverse

Olive-Buff (R. Pl. 40) to Pale Olive-Buff (R. Pl. 40) and at one month Deep Olive-Buff (R. Pl. 40); odor none; sporangiophores to 30 μ in width and variable in length, not septate, arising from stolons opposite rhizoids, erect, some simple, others branched typically dichotomously, brown in color; sporangia 50–160 μ in diam, at first white then black, breaking, smooth; columellae 30–70 μ in diam in globose ones to 122 $\times$ 132 μ for the large oval ones but mostly 70 $\times$ 90 μ or less, others dorsiventrally flattened, oval or spatulate, bluish gray, granular contents, collar absent or poorly defined; stolons to 16 μ in diam, smooth, hyaline to light brown; rhizoids hyaline to light brown and branched; sporangiospores 4.5–11 μ in size, but some up to 8 $\times$ 17 μ in irregular ones, heavy-walled, light gray singly, roughly globose but also angled and larger ones short oval to irregular, contents homogeneous; sporangiospore wall striate, smooth to faintly roughened; chlamydospores, oidia, etc. not seen even at one month; zygospores 70–175 μ in diam, globose to compressed between suspensors, coal black, covered with blunt spines up to 6.5 μ in length; suspensors 60–93 μ in diam, equal or nearly so, globose or ovoid, brown, surface slightly granular appearing but not roughened; zygospores formed typically between branches of same filament and the filament extended beyond as a sterile projection cut off by a septum; zygophores to 16 μ in diam, hyaline, smooth to faintly roughened; azygospores sometimes seen, brown to black, 60–100 μ; homothallic; no growth at 37° C.

TYPE strain: NRRL 2567. This culture, which originated from Mr. George Smith, was secured from the Centraalbureau voor Schimmelcultures, Baarn, Holland. Smith states that it was isolated in 1922 from a rotting strawberry at Cambridge, England. Kominami et al. (**1952**) reported the isolation of the same species from cherry (*Prunus yedoensis*) Meiji Shrine, Tokyo, Japan, by Kominami in 1950, and the species is said to be easily collected in Tokyo on cherry.

The above description is based on studies of the type strain NRRL 2567 on SMA at 25° C. On Czapek's solution agar growth is thin but within 5 days a few mature sporangia and a few zygospores are present. On malt extract agar the strain covers the agar but never reaches a height sufficient to touch the lid of the petri dish. The top of the colony (0.5 cm) has numerous sporangia with the zygospores formed beneath them. On PDA the growth is similar to that seen on malt extract agar, that is, the colonies are gray and the reverse is gray.

In 1957, we received a homothallic *Rhizopus* from Dr. C. T. Rogerson for identification. At the time we identified it as *R. sexualis*, but we noted that in some respects it showed considerable differences from the type strain. This was reported by Kramer et al. (**1960**) as *R.*

sexualis. Further study of this strain through a number of generations has led us to conclude that this isolate represents a new variety of *R. sexualis.*

RHIZOPUS SEXUALIS var. **americanus** Hesseltine & Ellis, var. nov. FIGS. 17–18

Sporangiophora usque 16.5 μ in diam., simplicia; sporangia 40–75 μ, globosa; columellae 15–45 μ; sporangiosporae 6.5–8 × 7–11 μ, substriatae; zygosporae 60–235 μ, mediae circa 170 μ, atrobrunneae usque atrae, processibus 12 μ longis tectae; suspensores aequales vel subaequales; species homothallica; ad 37° C non crescens; ex aere isolatus.

Colonies 1–2 mm in height, rapidly growing, at first white then gray, uniform except for white aerial mycelium at point of inoculation, colonies speckled because of black zygospores, near Slate Black (R. Pl. 53) later Mouse Gray (R. Pl. 51) at 1 month; colony reverse Light Olive-Gray (R. Pl. 51) with the zygospores showing through the agar; odor none or faint; sporangiophores to 16.5 μ in diam, typically 400–1100 μ in length, arising opposite rhizoids, 1–3 in a place, never branched, colorless to light brown, smooth-walled, usually not septate, erect, or growing horizontally; stolons smooth-walled, hyaline, to 15 μ in diam; rhizoids light brown to hyaline at their ends, sometimes septate, poorly branched, to 10 μ in diam; sporangia 40–75 μ, at first white then gray in reflected light, globose, many-spored, breaking with spores lying loosely on columellae, apophysis not clearly seen; sporangial wall thin, transparent; columellae 15–45 μ in diam, smooth-walled, globose, dorsiventrally flattened to larger ones ovoid, hyaline to very light brown, collar none; sporangiospores variable, globose 5–11 μ to oval 6.5–8 × 7–11 μ and in irregular ones to 9 × 15 μ, contents uniform to vacuolate, hyaline to very light yellow brown; sporangiospore wall thick, faintly striate; giant cells in substrate mycelium to 50 μ in diam, intercalary, hyaline, smooth-walled, globose to irregular in shape, empty or filled with yellowish granular cytoplasm; chlamydospores absent; zygospores variable in size, 60–235 μ in diam, average near 170 μ, globose or compressed between suspensors, blackish brown to black, found immediately above the surface of agar and below sporangia; zygospore wall roughened with projections that are pointed to blunt and flattened, projections to 12 μ in length, zygospores borne on zygophores and surrounded with droplets of exudate, sometimes between branches of same zygophores, others between different zygophores; zygophores smooth, up to 15 μ or more in diam; suspensors equal or nearly so, borne parallel to each other, smooth, with granular contents, globose swollen or slightly compressed in long axis, brown in color, swollen portion 30–140 μ in diam; homothallic; no growth at 37° C.

TYPE strain: NRRL 2626, isolated from air, Manhattan, Kansas, June 3, 1957.

The description was prepared from study of this strain at about 10 days at 25° C on SMA. The colonies grow very rapidly, reaching a diam of 14 cm in 3 days. At the margin of the growing colonies stolons and rhizoids are seen with rhizoids at points where stolons touch the agar. Both zygospores and sporangia are formed simultaneously immediately back of the colony margin. The zygospores are formed in the same manner as those of *R. sexualis,* and with aging the outer swollen portions of the suspensors collapse inward.

Unlike *R. sexualis,* which grows and fruits on Czapek's solution agar, this variety produces only a few filaments at point of inoculation and then growth ceases. On media, such as malt extract agar, growth is luxuriant and reaches a height of 1–2 mm; the plate is speckled gray because of the uniform production of zygospores. Intermixed is sterile mycelium and above this are numerous unbranched sporangiophores with small sporangia. The reverse of the colony is pale yellowish gray. Growth on PDA is similar to that on malt extract agar, but the reverse of the colony is gray.

This variety is distinguished from the type variety of *R. sexualis* by having (1) much smaller sporangia, (2) sporangiophores never divided, (3) colonies uniform in appearance, (4) sporangiospores more faintly marked with striations, (5) zygospores much larger and (6) giant cells fairly numerous in the substrate mycelium.

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NOTES ON WESTERN RUST FUNGI I. CHRYSOMYXA

Roger S. Peterson [1]

During studies of forest tree rusts in the central Rocky Mountains, information on distribution, occurrence, and life cycles of various Uredinales has developed incidentally to major projects. It is planned to report such material in the present series. This first paper offers a solution to some problems regarding the life cycle of *Chrysomyxa arctostaphyli* Diet., cause of spruce broom rust, and gives distributional records for two other Chrysomyxae.

Thanks for access to herbaria are due to C. R. Benjamin (National Fungus Collections), G. B. Cummins (Purdue Univ.), J. W. Baxter (Univ. Wisconsin, temporarily at Purdue), and W. G. Solheim (Univ. Wyoming). Cited specimens are filed at the National Fungus Collections and at the U. S. Forest Service forest disease laboratory in Fort Collins, Colorado.

The central Rockies have few representatives of *Chrysomyxa*; Colorado, for instance, is known to have only two species: *C. arctostaphyli*, which is common on aecial and telial hosts, and *C. pirolata* Wint., which is common on *Pyrola* but rarely seen on *Picea* cones in the state. This paucity of species compares, for example, with six in New Hampshire, seven in Alaska, and ten in British Columbia (**1**, **2**, **8**, **9**). A report of *C. ledicola* Lagh. on spruce in Colorado (**11**) is probably an error: the telial hosts are not known in the state, the record was not properly documented in files of the Agricultural Research Service on which this reference is based, nor could I find a specimen. Other questionable Rocky Mountain records are given for *C. arctostaphyli* (as *Melampsorella caryophyllacearum* Schroet.) in a world monograph (**4**); for instance, the occurrence of this rust on Sitka spruce in New Mexico and South Dakota is unlikely because of environmental requirements of the host. Perhaps these records are based on a confusing entry in the Weiss and O'Brien index (**11**, p. 336).

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CHRYSOMYXA ARCTOSTAPHYLI Diet.

1. Telia on *Arctostaphylos patula* Greene; Arizona, Grand Canyon National Park, North Rim, Cape Royal Road at 8600 ft. elev.; May 29, 1961; R. S. and M. L. Peterson 36–61.

Teliospores in the most nearly mature layer measured, for the most part, only 6–10 × 15–20 μ, with only a few attaining minimal dimensions (13 × 23 μ) given by Arthur (1) for the species. This is surely a result, not of morphologic differences, but of immaturity: no telia had yet ruptured the host epidermis. Telia were amphigenous, in contrast with those on *A. uva-ursi* (L.) Spreng. (bearberry), which are almost exclusively hypophyllous. Perhaps this difference is related to the absence of stomata on upper leaf surfaces of *A. uva-ursi,* and their presence on both surfaces in *A. patula.*

This collection on a new host appears to solve a major problem in the distribution of spruce broom rust, namely, unexplained occurrence of the aecial stage on spruce many miles southward of the range of the known telial host, *A. uva-ursi* (7). On the North Rim in Arizona, *C. arctostaphyli* infects both blue and Engelmann spruces, causing multiple witches'-brooms and trunk infections in many stands. *A. patula* (greenleaf manzanita) is abundant near most of the damaged stands and probably occurs at least sparsely in or near all of them. Collecting in four areas near spruce, we found telia on 49 of the first 50 bushes inspected.

2. Telia on *A. patula*; Utah, Dixie National Forest, near Utah Route 14 south of Hatch; June 1, 1961; R. S. and M. L. Peterson 46–61.

A new host for Utah, in an area where *A. uva-ursi* is scarce or lacking. The rust was also collected on this host at 8500 ft. elev. near Ephraim, Utah.

3. Telia on *A. patula*; greenhouse inoculations at Fort Collins, Colorado; September 27, 1961; Peterson 142–61.

Two healthy *A. patula* bushes were transplanted from the Dixie National Forest to a greenhouse at Fort Collins in early June, 1961. After two months they still showed no sign of rust. On August 3 fresh aeciospores of *C. arctostaphyli* (Peterson 116–61, from *Picea engelmannii* in southeastern Wyoming) were applied to the leaves of one of them in a moist chamber. When next checked (September 7, 1961) the inoculated leaves were red-spotted and bore several telia (immature, because not yet given a "wintering" treatment). The control plant, which had also been in a moist chamber for three days and then kept on a bench with the inoculated plant, showed no sign of infection. This result is taken to support the identification of *C. arctostaphyli* on manzanita, and inci-

dentally—by the use of aeciospores collected far from any manzanita—shows that the manzanita rust is probably not a specialized race.

4. Telia on *A. nevadensis* var. *coloradensis* (Roll.) Harrington; Colorado, Uncompahgre National Forest, Uncompahgre Plateau south of Grand Junction at 9500 ft. elev.; July 5, 1961; Peterson 101–61.

Teliospores of the most nearly mature layer measured 8–13 × 14–37 μ. Host epidermis was broken, but basidia were not yet produced. This is a new host species for *Chrysomyxa.* Only two telia on opposite surfaces of one leaf could be found; but *A. uva-ursi* growing a few hundred yards closer to broomed spruce was heavily infected.

5. Telia on *A. uva-ursi* (L.) Spreng.; South Dakota, Black Hills National Forest, 8 miles west of Rochford at 5700 ft. elev.; June 14, 1961; R. S. Peterson and W. P. Schacht 69–61.

This is a first report of the telial stage from South Dakota, where aecial infection is common on white spruce in the Black Hills. Aecial and telial stages are usually clearly associated here, the spruce in valleys and bearberry on adjacent south-facing slopes.

6. Pycnia and aecia on *Picea glauca* (Moench) Voss; Wyoming, Weston County, near Buckhorn at 6200 ft. elev.; September 13, 1961; R. S. Peterson 138–61.

A new host species for Wyoming, where *P. glauca* (white spruce) is native in the Black Hills area. The telial stage on *A. uva-ursi* was abundant in the stand. This stage was first recorded from Wyoming by Wehmeyer (**10**).

7. Pycnia and aecia on *Picea pungens* Engelm.; Utah, Ashley National Forest, Uinta Mountains near Summit-Daggett county line west of Manila at 8200 ft. elev.; August 22, 1960; R. S. Peterson 217–60.

This is a newly recorded host species for Utah. Infection is relatively as frequent here as it is on *P. engelmannii* (Engelmann spruce), but *P. pungens* (blue spruce) is much less abundant.

C. arctostaphyli is now known from at least 25 North American states, provinces, and districts. It extends from coast to coast, and reaches its known extremes of latitude on *Picea glauca* at the Arctic circle (Fort Yukon, Alaska, collected by D. V. Baxter in 1935; specimen in W. G. Solheim Herbarium) and on *P. engelmannii* in the Sangre de Cristo Mountains near Santa Fe, New Mexico (unpublished field notes of both F. G. Hawksworth and L. S. Gill). Its altitudinal spread is from near sea level on both coasts to around 12,000 feet on spruce in Colorado.

The latter elevational extent was puzzling, and raised some doubt that *Arctostaphylos* could be the telial host, because records of *A. uva-ursi*

seldom exceeded 10,000 feet. Harrington records the plant "at 6000–10,000 feet" in Colorado (**3**). The highest known record of the telial stage was from southern Wyoming at 10,200 feet (W. G. Solheim 2184, issued as Mycoflora saximontanensis exsiccata 501). In many places the high spruce forests are miles from the abundant bearberry of the lower lodgepole pine type, and bearberry is not apt to be associated with the spruce itself. A day devoted to this problem in the vicinity of Independence Pass and Cottonwood Pass in central Colorado seemed to provide an answer, however. On the western flanks of Mt. Elbert bearberry occurs on disturbed ground up to 11,700 feet, and *Chrysomyxa arctostaphyli* was found on it nearly that high. Apparently the host's occurrence on raw stream cuts and earth slides, above and between subalpine spruce stands, saves us the necessity of postulating long-distance transmission of the rust by basidiospores.

My own observations of aecial and telial stages of spruce broom rust tend to confirm those of Savile (**8**) regarding the telial stage, that this fungus is much more abundant in the West than in eastern North America. *A. uva-ursi* occurs with spruce at lower elevations in both regions; I know of no explanation for the difference.

CHRYSOMYXA WEIRII Jacks.

1. Telia on *Picea glauca* (Moench) Voss; South Dakota; Black Hills National Forest, 8 miles west of Rochford at 5700 ft. elev.; June 14, 1961; R. S. Peterson and W. P. Schacht 70–61.

Unlike most widely distributed spruce rusts, *C. weirii* appears not to have a continuous range through the boreal and subalpine forests: it is known from the Pacific Northwest, the southern Appalachians, Ontario and the Maritime Provinces, and south central Asia (**1**, **5**, **6**, **8**). However, the present collection helps to fill in the great gap between known stations in western Ontario and northern Idaho, and is a host record for the United States. In the northern Black Hills it was abundant in several localities, with nearly all of the previous year's needles infected on the lower branches.

Teliospores measured $6–8 \times 18–31\ \mu$: a bit larger than Arthur's measurements (**1**), but like those of Savile (**8**).

CHRYSOMYXA PIROLATA Wint.

1. Uredinia on *Pyrola minor* L.; South Dakota; Black Hills National Forest, 8 miles west of Rochford at 5700 ft. elev.; June 14, 1961; Peterson 72–61.

A first record of the species for South Dakota, where it is quite common in the Black Hills. Although occurring near white spruce, rust was not found on cones.

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NOTES AND BRIEF ARTICLES

An Arthrobotrys from brackish water [1]

Fungus-animal associations in maritime environments vary from ecto-commensal relationships as, for example, the eccrinids in mole and mud crabs, to strictly pathogenic ones such as are developed in the case of *Ichthyosporidium* in teleost fish and the lagenidias in marine invertebrate ova. Numerous such associations have been described, for which the pertinent literature is reviewed by Johnson and Sparrow (**1961**). Among the reports summarized by these authors is a single reference to predacious fungi in a maritime habitat, that being the paper by Jones (**1958**) on a collection of three zoöpagaceous forms in brackish water. We report a second occurrence of predacious fungi in salt water, namely, a nematode-capturing hyphomycete.

Two collections of the fungus were made. In the first, the organism appeared on a pine panel (*Pinus taeda* L.) that had been submerged for 37 days in the oligohaline zone (±5–±0.5‰ salinity) of the Neuse River estuary, North Carolina, and subsequently incubated for two weeks in the manner described by Johnson and Sparrow (**1961**). The organism later occurred on a yellow poplar panel (*Liriodendron tulipifera* L.) submerged for 61 days in the mesohaline zone (±18–±5‰) of the same estuary. This panel was not incubated. Only the fungus on the incubated panel had captured nematodes; constricting rings were in evidence, however, on the hyphae of the specimen from the incubated panel.

A synopsis of the organism, assigned to the genus *Arthrobotrys* Corda, follows:

Hyphae hyaline, septate, sparingly-branched; 4–8 μ in diameter at base of conidiophores; occasionally contorted; producing loops at intervals. Hyphal loops lateral, consisting of three, hyaline, arcuate cells; attached by a short, 1- or 2-celled pedicel to main thread; loops occasionally double; unconstricted loops averaging 62 μ in diameter; constricting and forming one or two globose evaginations within a captured nematode, these evaginations giving rise to branched assimilative hyphae terminating in bulbous apices. Conidiophores erect, hyaline, sparingly-branched and septate; tapering toward an apical, globose expansion from which arise three or more cylindrical, truncate sterigmata; 180–460 μ

[1] The financial support of the National Science Foundation Grant, G-7178, is gratefully acknowledged.

long, 4–8 μ in diameter at base. Conidia hyaline, unequally 2-celled, fusiform-ellipsoidal to obpyriform; borne in a loose, capitate mass on the sterigmata; 28–40 × 7–12 μ.

The precise identity of the fungus and the captured nematodes remains in doubt, although the animals most often found in the constricting rings were members of the genus *Odontophora*. The fungus is tentatively assigned the name *Arthrobotrys dactyloides* Drechsler (**1937**: 486, fig. 6), even though the characteristics of our material diverge somewhat from the species concept evident in Drechsler's account. Principal points of digression are: (1) longer and more obvious sterigmata in our material than in Drechsler's fungus; (2) consistently unequal-sized conidial cells in our specimens; (3) their occasional double or proliferated constricting rings; globose conidiophore apices, and (4) branched assimilative hyphae arising from the intramatrical evaginations as contrasted with the unbranched ones described by the author of the species. Size differences between the fungus of our collection and that of Drechsler are not significant, in our opinion.

There is no intent, implied or otherwise, to convey the impression that the predacious *Arthrobotrys* is strictly limited to brackish water and can therefore be designated as a "salt-water fungus" or Thalassiomycete. Its habitat is unusual, but many other representatives of "terrestrial" genera also occur in maritime situations. Our collections merely show that predacious fungi are adaptable enough to exist and reproduce *submerged in saline waters*.—T. W. JOHNSON, JR. AND CHARLOTTE L. AUTERY, Department of Botany, Duke University, Durham, North Carolina, and the Marine Laboratory, Beaufort.

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PROLIFERATION OF CONIDIOPHORES AND INTRAHYPHAL HYPHAE IN ASPERGILLUS NIGER

Proliferation, or the successive development of new parts, of the sterigmata on the conidial head in the genus *Aspergillus* has been reported to occur in many species, especially *A. ruber* Bremer (**5**), *A.*

deflectus Fennell & Raper (**4**) and *A. proliferans* G. Smith (**6**). In the last species, proliferation occurs to such an extent as to be considered as the most conspicuous characteristic of the organism and will occur under optimum growing conditions. Generally, adverse conditions are

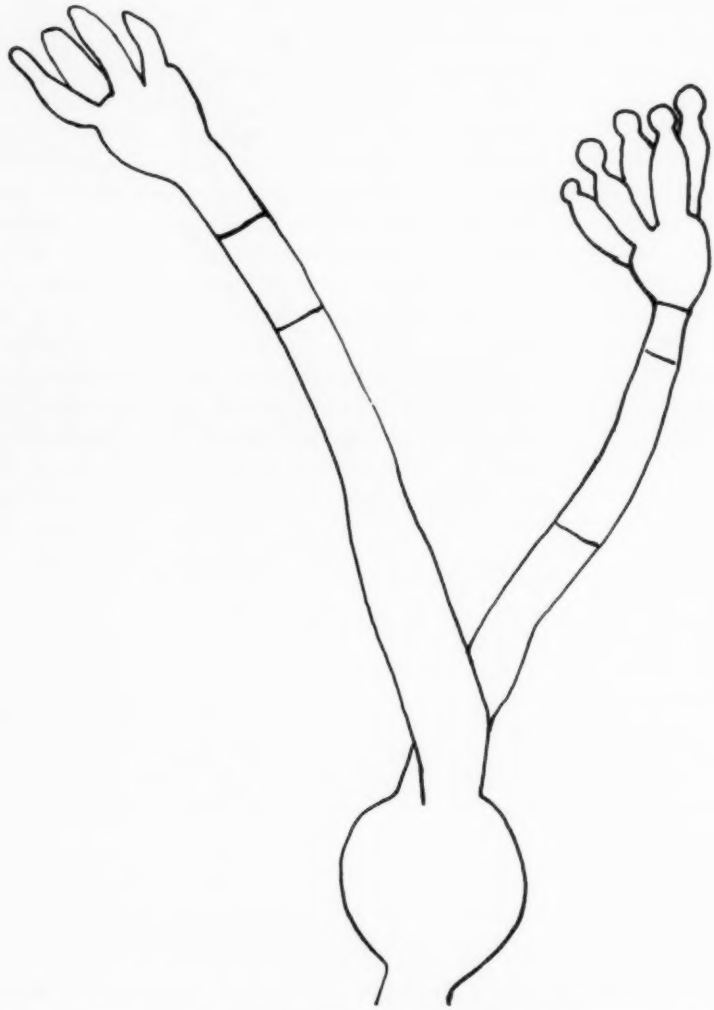

FIG. 1. *Aspergillus niger.* Proliferation of conidiophore when grown under nearly anaerobic conditions.

necessary for proliferation. It was recently observed by the senior author that conidiophores of *A. niger* van Tiegh. proliferated and that intrahyphal hyphae formed when the fungus was grown under nearly anaerobic conditions.

In this study a modification of the plastic bag technique developed by Den Ouden (**2**) was used. This consists of pouring water agar into plastic bags measuring 4 × 5 inches and restricting as much as possible the formation of air bubbles. The bag is placed between two pieces of glass maintained a constant distance apart to insure uniform thickness of agar and exposed to ultra-violet light (Westinghouse Sterilamp #782H-30) for 20 minutes. The technique described here was used to study root-rotting fungi and *A. niger* occurred as a contaminant.

The surface of the plastic was sterilized with alcohol and a small slit made in the bag through which inoculations were made. A strain of *A. niger* which developed normally on Czapek's agar medium was used

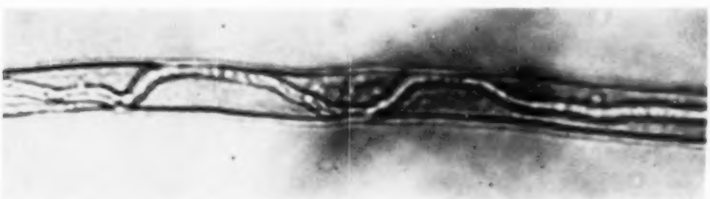

FIG. 2. *Aspergillus niger.* Intrahyphal hyphae growing within the mycelium of parent culture.

as the inoculum source and single germinating spores were placed on the agar surface within the plastic bag. The slit was then sealed with plastic tape.

One type of proliferation which occurred under these conditions is illustrated in FIG. 1. The sterigmata elongated and formed a second vesicle which in turn has produced normal conidia. In some instances, the sterigmata developed into hyphal filaments which branched and produced 1–3 sterigmata and short chains of conidia. Isolations from normal heads, proliferated heads and single sterigmata produced normal *A. niger* colonies when grown on Czapek's agar medium, suggesting that the morphological changes which were observed were the results of the environment in which the fungus was developing.

In addition to these proliferations, intrahyphal hyphae were observed. It has been reported by Buller (**1**) that often in hyphae one or more cells die and the remaining living cells produce slender hyphae which grow

through the adjacent dead cells intrahyphally. This phenomenon has been reported to occur in *Saprolegnia, Ascobolus, Gymnosporangium, Botrytis* and *Rhizoctonia* (**1**, **3**); however, it has not been reported previously in the genus *Aspergillus*. An example of the intrahyphal hyphae is illustrated in FIG. 2. In repeating this work, strands of hyphae in which this occurred were removed from the bag and placed on agar in petri dishes. The intrahyphal hyphae grew out of the dead hyphae and produced normal hyphae and conidiophores of *A. niger*.

In a few instances the intrahyphal hyphae were observed to form conidiophores within the walls of the dead cells (FIG. 3). The vesicles were greatly reduced in size, possibly a result of confinement within the walls of the dead cells, and sterigmata were reduced to a single series. A limited number of spores were found attached to these sterigmata, and some were found free in the mycelium. To the authors' knowledge this

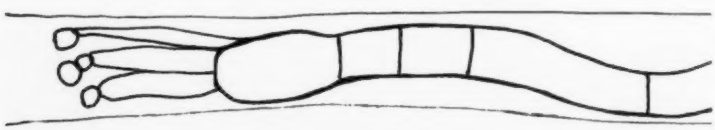

FIG. 3. *Aspergillus niger*. Formation of conidiophore by the intrahyphal hyphae within the mycelium of parent culture.

is the first time that intrahyphal hyphae have been reported in the genus *Aspergillus* and the first time that such hyphae have been observed to produce conidiophores while still within the walls of the dead mycelium.
—C. W. MILLER AND N. A. ANDERSON, Department of Plant Pathology, University of Minnesota, St. Paul 1, Minnesota.

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ILLUSTRATION OF ELSINOË BOUCHEAE

The figure designed to accompany my formal description of *Elsinoë boucheae* [1] somehow became lost following its use to illustrate my paper, "A spot disease of *Bouchea* in Cuba." [2] I owed the composite figure to my colleagues, Anna E. Jenkins and A. A. Bitancourt, to whom I am again grateful for its reconstruction following the original design (FIG. 1). My collection (A. G. K. 412, correct date 1946) serving as the

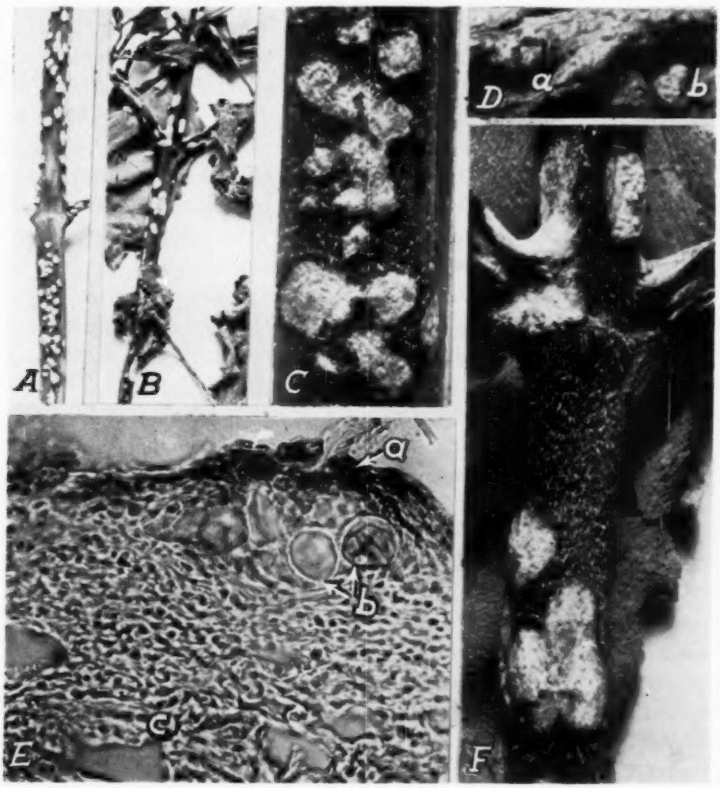

FIG. 1. *Elsinoë boucheae*. A and B. Stem infection. × 1. C. Lesions from A. × 5. D, *a* and *b*. Leaf spots, ascomata of the *Elsinoë* forming dark rings. × 10. E. Ascoma on a petiole lesion. × 500. F. Part of B. × 5. TYPE specimen.

[1] Kevorkian, A. G. 1960 [1961]. *Elsinoë* on *Bouchea prismatica* in Cuba. Mycologia **52**: 523–524.

[2] Abstract in Phytopathology **43**: 406. 1953.

type of *E. boucheae,* besides being deposited as stated in the description, was in sufficient quantity for distribution in the Jenkins & Bitancourt Myriangiales selecti exsiccati (Fasc. 10, No. 457.)—ARTHUR G. KEVORKIAN.

SCLERODERMA POISONING

Most works dealing with edible and poisonous mushrooms label species of the genus *Scleroderma* as suspect, undesirable, or inedible and in some instances as actually poisonous. McIlvaine, that most noted of American mycophagists, states on the contrary (*One Thousand American Fungi,* p. 616, 1902), "Sliced and well-cooked the species [*S. aurantium*] is good, even after it has become purplish." Murrill (Mycologia **2**: 4. 1910) notes, "I have eaten *S. aurantium,* but do not consider it attractive." Hard (*Mushrooms,* p. 556. 1908) in discussing this species says, "Edible . . . not poisonous as it is generally thought to be; however, it cannot be claimed as a very good article of food." In contrast there is an account in the Gardner's Chronicle for 1868 (pp. 989–990) of severe gastric disturbances suffered by four persons in England who ate small quantities of *S. vulgare* (= *S. aurantium*) with comment by M. J. Berkeley on the edible properties or otherwise of the white fleshed (*Lycoperdon, Calvatia*) and the purple fleshed (*Scleroderma*) puffballs.

European mushroom manuals rather uniformly label the genus as poisonous or at least as nonedible. Pilat (*Mushrooms,* text for plate 6. 1954) definitely records for *S. aurantium,* "Poisonous mushroom! Eaten in any quantity it causes lighter or stronger poisonings, showing themselves by a feeling of uneasiness, vomiting, perspiration, and unconsciousness. Eaten in smaller quantities as seasoning it is, however, quite innoxious and lends the food a pleasant aromatic taste resembling the taste of truffles. It is therefore used as a substitute for real truffles . . . The sausagemakers in Prague and elsewhere . . . use it for 'truffle sausages' and even in the most exclusive restaurants it is used in the kitchen." Rolfe and Rolfe (*Romance of the fungus world.* 1925) and Ramsbottom (*Mushrooms and toadstools.* 1953) make substantially similar statements as to the use of *Scleroderma* as an adulterant of or substitute for true truffles. They do not condone its use in this manner.

At the National Fungus Collections we have had, through the years, various accounts by individuals who claimed to have eaten one or the other of the species of the genus with serious results as well as one clear-cut report of serious illness produced by a small amount of *S. aurantium*

cooked and eaten experimentally. The victim was a physician who was able to give us a detailed account of her experience.

Recently there came to our attention a case involving *Scleroderma cepa* Pers. No previous accounts dealing with the attempted use of this species for food have been found. A young man cutting a neighbor's lawn in the early morning hours of a Sunday noticed an interesting appearing puffball and remembering that the mushroom manuals agreed that all puffballs were edible, took a small bite and said later that it tasted good. He had neglected, of course, to read the qualifying clause which warns "as long as the flesh within is firm and white." Within thirty minutes stomach pains began, followed rapidly by a general feeling of weakness and nausea without dizziness but with a tingling sensation over the entire body. Muscles became rigid, the sensation passing up the patient's arms and soon involving the extremities. With the entire body rigid, the victim managed to reach the door of the home and to arouse the man of the house who drove him at once to a hospital, reaching there within 45 minutes of the time of ingestion. By this time tetany (muscle rigidity) was far advanced, accompanied by stomach cramps, profuse sweating, and distinct facial pallor. He was removed from the car with difficulty and carried into the hospital. The only medical assistance was that of an intern who attempted to insert a stomach tube first orally and then through the nose but failed because of muscle contraction. The patient, who had not lost consciousness, finally managed to make known his wish to be turned over on his stomach and was then able to force himself to vomit. He experienced prompt relief, all symptoms cleared up rapidly, and he was shortly released without any medical treatment having been given. A check-up by his own physician on the following day showed no undesirable after effects.

In view of cases with unpleasant results such as the one just recorded it would seem highly desirable to avoid use of species of *Scleroderma* as food, either raw or cooked, in spite of reports to the contrary that members of the genus have been eaten with impunity.—JOHN A. STEVENSON AND CHESTER R. BENJAMIN, National Fungus Collections, Crops Research Division, Beltsville, Maryland.

PRODUCTION OF LARGE SOLITARY SPORANGIOSPORES IN SOME SPECIES OF THE MUCORALES

Several maize-meal-agar plate cultures to which had been added small pinches of leaf mold newly collected in a wooded area near College Park in central Maryland on July 15, 1955, showed 14 days later some

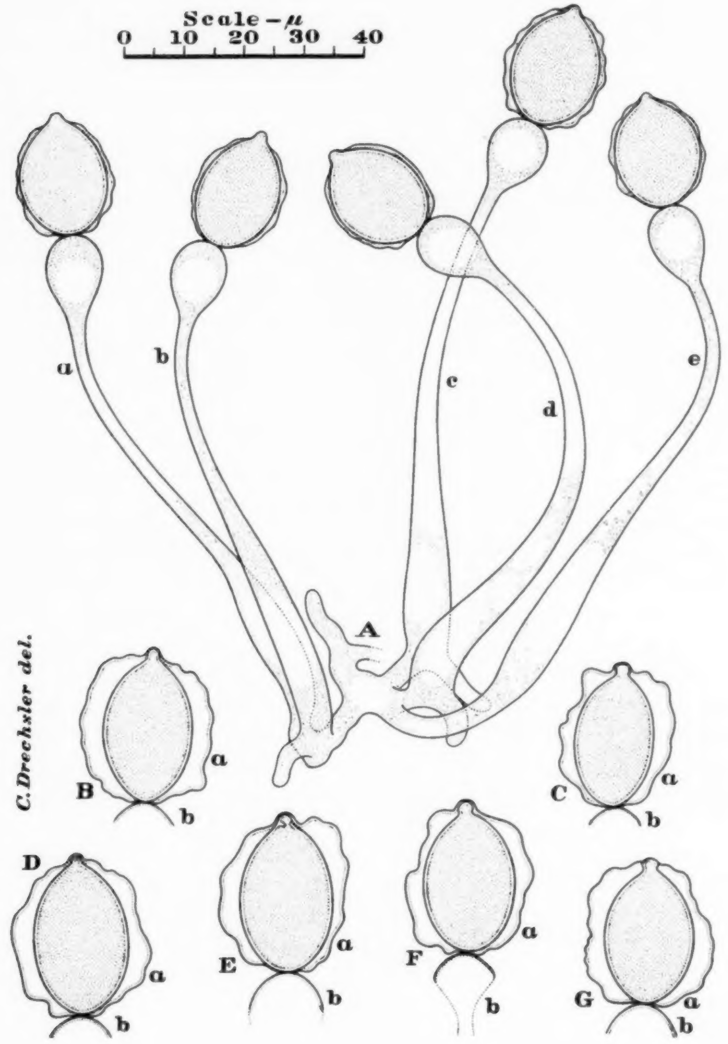

FIG. 1. Monosporous sporangial stage belonging presumably to *Syncephalis* sp., × 860. A, Group of 5 sporangiophores, a–e, each bearing a monosporous sporangium. B–G, Six monosporous sporangia, a; each shown attached to a persistent apical portion of sporangiophore membrane, b.

few sporangiophores arising singly or in small groups (FIG. 1, A, a–e), each bearing on the apex of an obovoid distal enlargement a solitary ovoid spore loosely surrounded by a somewhat collapsed sporangial membrane. The sporangiophores ranged from 85 to 100 μ in length and in many instances were rather markedly curved. From a swollen basal portion usually 6 to 8 μ in diameter they tapered gradually upward to a width of approximately 2.2 μ. This width they maintained for a distance of 20 to 25 μ and then expanded rather abruptly into the obovoid distal enlargement, which commonly measured 12 to 14 μ in length and 8.5 to 10 μ in greatest diameter. The solitary spore borne in axial alignment with the enlargement was colorless or faintly brownish. Within its proper wall, about 0.6 μ thick, was contained dense protoplasm of finely granular or nearly homogeneous appearance. It usually measured 13 to 16 μ in greatest width and 19 to 27 μ in length inclusive of a wart-like apical protuberance 1 to 2 μ long and 2 to 2.5 μ wide. The loose sporangial envelope (FIG. 1, B–G: a), which often showed many parallel transverse striations, was affixed distally to the upper surface of the protuberance, while proximally it seemed attached not only to the tip of the sporangiophore (FIG. 1, B–G: b) but also to the base of the surmounting spore. In moist preparations a small apical portion of the sporangiophore (FIG. 1, B–G: b) usually persisted for some time after the tubular membrane had faded from sight.

Asexual reproductive apparatus of generally similar make-up has now and then come under observation also in Petri plate cultures inoculated with plant detritus from other localities in central Maryland, as well as in cultures to which had been added slowly decaying materials from more distant places in both the southeastern and northwestern regions of that State. In many cultures the sporangiophores bearing the solitary spores were found sparsely intermingled with other sporangiophores, which, though of rather similar stature and shape, differed markedly in that they bore circularly arranged on the shoulder of the distal enlargement from 4 to 6 digitate branches, or merosporangia, each containing a chain of 2 elongated spores. The inference could hardly be avoided that the monosporous sporangia represented accessory reproductive bodies of species of *Syncephalis* related especially to *S. tenuis* Thaxter (**1897**) and *S. nana* Dade (**1938**). However, owing to the decrepit condition of the underlying mycelium and to the presence of many other microorganisms—all of the cultures had been prepared primarily for the study of nematode-destroying fungi—it was never possible either to trace a hyphal connection between one-spored and many-spored sporangiophores or to ascertain that such connection was absent.

Because of its relatively dense contents, its somewhat thickened wall, and its usual failure to germinate on moist substratum, the solitary spore would seem adapted for survival through prolonged unfavorable periods. As it receives a quantity of protoplasm that elsewhere is manifestly sufficient for the development of a circlet of two-spored merosporangia, it must be considered a less elementary reproductive body than the unisporous sporangioles of *Chaetocladium* or of *Haplosporangium decipiens* Thaxter (**1914**). Except for the likelihood that in eventually germinating it might put forth a typical *Syncephalis* sporangiophore the solitary spore, together with the membrane loosely surrounding it, is perhaps nearly equivalent morphologically to the conidium of *Rhopalomyces elegans* Corda, which Boedijn (**1927**) found to be multinucleated and accordingly interpreted as a merosporangium incapable of forming sporangiospores. —CHARLES DRECHSLER, Crops Research Division, Agricultural Research Service, United States Department of Agriculture, Plant Industry Station, Beltsville, Maryland.

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